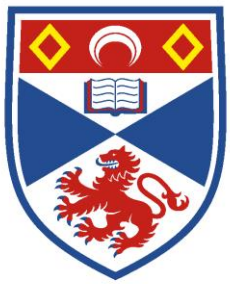
# An investigation of teaching behaviour in primates and birds

Camille A. Troisi



University of
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26/08/2016

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# General Abstract

Many animals socially learn, but very few do so through teaching, where an individual modifies its behaviour in order to facilitate learning for another in individual. Teaching behaviour is costly, but can confer numerous advantages, such as high fidelity transmission of information or an increase in the rate of social learning. In many putative cases of teaching, it is not known whether the pupil learns from the modified behaviour. This thesis addresses this issue in three cases of potential teaching behaviour.

In particular, it investigates whether the role of food transfers in wild golden lion tamarins is to teach which foods are good to eat (**Chapter 5**). There was little evidence that novel foods were transferred more than familiar foods, and this was not due to the juveniles attempting to obtain novel foods more than familiar ones, or by adults discarding novel foods more than familiar ones. Transfers were however more successful when donors had previously ingested the food type transferred. Successful food transfers also had a positive correlation with foraging choices once juveniles were older, suggesting they learned from food transfers.

In golden lion tamarins, this thesis also examined whether juveniles learned from food-offering calls which substrates were good to forage on (**Chapter 6**). Juveniles that experienced playback of food-offering calls ate more on a novel substrate, than juveniles that did not experience those playbacks, both immediately as the calls were being played, and in the long term, six months after the playbacks. This suggests that juveniles learned from the playbacks.

Finally, this thesis attempted to replicate previous findings showing that hens modify their behaviour when chicks feed from seemingly unpalatable food, and explored whether chicks learned what food to eat based on the maternal display (**Chapter 7**). The experiment failed to find evidence for teaching behaviour, but results were not inconsistent with previous findings. Moreover, there was little evidence that chicks learned from their mother, quite to the contrary, hens seemed to acquire their foraging decisions based on their chicks' choices.

# Chapter 1:

# General Introduction

Teaching is one of many forms of social learning in which knowledge or skills are passed from one individual to another. It is an important process in human development and culture (Laland, 2017), and for a long time it has often been seen as a uniquely human behaviour. However, in more recent years, a few strong cases and many suggestive cases of teaching in non-human animals have begun to raise questions about previous assumptions about teaching. The aim of my thesis is to study three putative cases of teaching, and particularly examine whether observers acquire knowledge from the demonstrators' (putative tutors) modified behaviour. The approach used in this thesis to study teaching is the functionalist approach, as it is the most widely used in the field of animal behaviour. However, as Kline (2015) and Hewlett (Hewlett, Fouts, Boyette, & Hewlett, 2011; Hewlett & Roulette, 2015) point out, there is wide disagreement between fields and researchers as to what constitutes teaching. I will therefore begin by describing how a functional perspective leads to a definition of teaching, and then discuss some complications and amendments, before going over the definitions of teaching deployed in other fields of study. I will then report some theoretical and empirical findings concerning the evolution of teaching. Finally, I will review evidence of teaching in non-human animals, based on a definition derived from the functionalist approach.

## 1.1 Definitions of teaching behaviour

Some researchers consider teaching to be a uniquely and universally human attribute, while others think that only Western societies teach, and some authors have documented teaching in non-human animals (Kline, 2015). This shows that teaching does not have a widely accepted definition, and that what exactly constitutes teaching is still debated (Byrne & Rapaport, 2011; Csibra, 2007; Hoppitt et al., 2008; Kline, 2015; McAuliffe & Thornton, 2012; Premack, 2007; Rapaport & Byrne, 2012; Thornton & Raihani, 2008; Thornton, Raihani, & Radford, 2007). Teaching has been differentiated from other social learning forms in several different ways. Many psychologists have differentiated teaching from social learning based on intent, while animal behaviourists will set teaching apart based on the active change in behaviour of the tutor, regardless of

intentionality. Intent is difficult to study in non-human animals because they do not have language, and so cannot report on their intent. That is why the functional approach is used in my thesis to study the potential teaching behaviour in birds and primates, so that it can be based on measurable and observable behaviour.

### 1.1.1 Functional approach: Caro and Hauser (1992)

From a functional perspective, teaching is a behaviour that functions to facilitate the transmission of information (skills or knowledge) between individuals, regardless of the proximate mechanisms involved (Hoppitt et al., 2008). Early descriptions of teaching behaviour date from the 1960s where Barnett (1968), in order to distinguish it from other forms of social learning, proposed two criteria to define teaching: (1) the behaviour of the tutor must result in changes in the behaviour of the pupil and (2) teaching must be adapted to the pupil's skill level and maintained until a certain level is acquired. However, as Ewer (1969) points out, this definition does not differentiate active teaching from inadvertent social learning. It was not until 1992 that a functional definition of teaching which made this distinction was provided by Caro and Hauser (1992).

In order to detect teaching, Caro and Hauser (1992) created an operational definition, which is now widely used in the field of animal behaviour because it allows the animal's behaviour to be detected and measured based on observable criteria. This is the definition that I use in my thesis. According to Caro and Hauser (1992), "*an individual actor A can be said to teach if it modifies its behaviour only in the presence of a naive observer, B, at some cost or at least without obtaining an immediate benefit for itself. A's behaviour thereby encourages or punishes B's behaviour, or provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all*" (p. 153). Consequently, there are three criteria which allow one to identify a behaviour that functions to impart knowledge or skills to others. First, the

demonstrator (A) needs to modify its behaviour only in the presence of the naive observer (B); hence, the demonstrator, A, behaves differently in the observer's, B, absence. This first criterion allows distinguishing teaching from situations where the demonstrator engages in "normal" behaviour and the observer learns a behaviour by being in the presence of the demonstrator (e.g. stimulus enhancement or social facilitation), where learning is not the main but a secondary function of the behaviour (e.g. in sexual displays). Moreover the presence of a naïve observer is necessary to distinguish teaching from cases where the behaviour is rarely performed, regardless of the audience (Caro & Hauser, 1992). Second, this modified behaviour must incur a cost to the demonstrator, or at least no direct benefit. This cost can widely vary between species, individuals and context, and can be much greater than the cost of a lost opportunity created by the change in behaviour (Caro & Hauser, 1992). This second criterion allows one to distinguish teaching from cases such as aggression or weaning, where although the tutor modifies its behaviour, and the naïve observer learns (to avoid the winner of the fight or to become independent), learning appears to be a secondary consequence of the immediate benefit acquired by the putative tutor (access to resources in the case of aggression, or reduction of resource provisioning in the case of weaning) (Caro & Hauser, 1992). Finally, as a result of A's modified behaviour, the naïve observer B acquires either knowledge or skills that it would not have learned otherwise, or would not have learned as rapidly. This third criterion allows one to distinguish teaching from other social interactions. Together those three criteria allow researchers to identify whether a behaviour functions to promote learning in a naïve individual.

Caro and Hauser's (1992) functional approach to teaching is based on an evolutionary perspective and allows for the separation of the functional and mechanistic levels of explanation (Byrne & Rapaport, 2011; Kline, 2015; Thornton & Raihani, 2015). Hence, in this definition assessing the mental states of the tutor or pupil, or their intentions, is not necessary to establish whether a behaviour functions to impart knowledge in order to determine that teaching is occurring (Kline, 2015; Ziv, Solomon, & Frye, 2008).

### 1.1.2 Amendments to Caro and Hauser's (1992) definition

Some refinements and modification to Caro and Hauser's (1992) definition have been proposed by imposing additional criteria to the original definition. However, few have been widely accepted.

#### 1.1.2.1 Feedback

Caro and Hauser's (1992) first criterion stipulates that the tutor needs to modify its behaviour in the presence of a naïve observer, but there is no precision as to whether the tutor needs to tailor its behaviour to the skills or knowledge of the naïve individual. After conducting experimental work based on Caro and Hauser's (1992) definition, some authors have argued that feedback between the tutor and pupil is necessary for a behaviour to be considered teaching (Franks & Richardson, 2006; Richardson, Sleeman, McNamara, Houston, & Franks, 2007). Feedback would allow tutors to adjust their demonstration to the pupils' needs. This criterion is exemplified in Franks and Richardson's (2006) findings of teaching in tandem-running ants (*Temnothorax albipennis*). However, in other examples of teaching behaviour, even if the pupils are monitored, no direct feedback is necessary [e.g. meerkats (*Suricata suricatta*) (Thornton & McAuliffe, 2006)]. In fact, meerkats use the age of the pups rather than the pups' skills to assess what prey type to give them. The helpers sometimes also respond to the pupil's behaviour by nudging the prey towards them if the young ignore it. But the feedback is not necessary for the helpers to provision the pupil with different types of prey, and the nudging appears to be a "tweak" to make teaching more effective in some cases. Hence feedback does not seem necessary for tutors to adjust their behaviour. Franks and Richardson (2006) suggest that this criterion would help differentiate between teaching and other forms of communication. However, as Leadbeater et al. (2006) point out, no learning is involved in other forms of signalling in ants where feedback is used (the third criterion of Caro and Hauser's, 1992, definition), hence this criterion does not help distinguish the teaching behaviour from other communication forms, and might therefore be considered unnecessary.

#### 1.1.2.2 Type of information

Other authors have argued that the term "teaching" should be restricted to describing the passing of skills, concepts, rules and strategies rather than declarative knowledge, such as location of food (Csibra, 2007; Leadbeater et al., 2006). If declarative knowledge is being transmitted from one individual to another (e.g. the location of a place), and the tutor is active, Leadbeater et al. (2006) suggest that this behaviour should be called "telling" rather than teaching. They base their argument on the different functional consequences telling and teaching have: telling is specific to one context, whereas teaching allows an individual to solve a problem in multiple situations. The distinction therefore hinges on whether the learning in the pupil is short- or long-term. Leadbeater et al. (2006) specifically suggest that tandem-running in ants and the waggle dance in honeybees (*Apis mellifera*) should be classified as telling. Richardson et al. (2007) agree that the bees' behaviour can be considered telling as it provides factual information about a location, but disagree for the case of tandem-running ants. According to them the information transferred is not factual because both individuals are engaged in the action of the run, and the aim of tandem-running is not to bring the follower to a specific location, because there are more efficient ways to do this, but to enable it to return there several times independently. Moreover, there is bi-directionality in tandem-running, but communication in the waggle dance is only mono-directional. However, in the absence of clear agreement over whether specific examples of animal behaviour are teaching or telling, this definition has not been widely adopted (Hoppitt et al., 2008). Separating telling from teaching would also require most of human teaching to be re-categorised as telling.

#### 1.1.2.3 Cost criterion

One other amendment of Caro and Hauser's (1992) definition regards the second criterion: the cost of the modified behaviour. The cost could be so small as to be of no adaptive significance and not enable the differentiation between a behaviour that evolved for teaching or one that evolved for another function,

with teaching as a by-product (Hoppitt et al., 2008; Rapaport & Byrne, 2012). The cost to the putative tutor could even be very high, but the primary benefits to the putative pupil could be different from knowledge gain (Hoppitt et al., 2008). Food provisioning, especially in the case of tolerance, is often referred to in the context of the cost criterion. Food provisioning can provide the double function of providing nutritional value to the beneficiary as well as transferring information about foods. If a behaviour pattern increases the fitness of the tutor irrespective of whether the pupil learned, then Hoppitt et al. (2008) argue that evidence that the behaviour was modified to promote learning is necessary. For instance, meerkats transfer preys in different conditions of mobility (dead, disabled or intact) to their offspring (Thornton & McAuliffe, 2006). If provisioning solely served a nutritional purpose, it would be more efficient for adults to kill the prey and give it directly to the offspring. Hence in this case, evidence suggest that the provisioning pattern functions to facilitates learning (Kline, 2015), where teaching could allow the young to become independent earlier in life, or reduce danger in learning to forage.

### 1.1.3 Other views on teaching behaviour

Teaching was often thought to be uniquely human (Tomasello, Kruger, & Ratner, 1993), but Caro and Hauser's (1992) definition based on observable changes in behaviour has allowed the study of teaching behaviour in non-human animals to proceed. Definitions other than Caro and Hauser's (1992) have been proposed, mainly to explain teaching specifically in humans. All definitions other than Caro and Hauser's (1992) are conceptual rather than operational, and they vary according to the field and the questions of focus. While Caro and Hauser's (1992) definition does not propose any specific mechanism for teaching to occur, the other approaches often have a particular mechanism embedded in their definition. The definitions that have been proposed in different fields are also sometimes incongruent (Strauss & Ziv, 2012).

#### 1.1.3.1 Natural pedagogy: Csibra and Gergely

The functionalist approach focuses on the costs and benefits of teaching behaviour to explain its evolution and allow for cross-species comparisons (Kline, 2015). However, some authors think that what is lacking from Caro and Hauser's (1992) functionalist framework is an explanation of the unique features of teaching in humans compared to non-human animals. Csibra and Gergely (2006, 2009, 2011) define a novel form of teaching unique to humans, drawing on the same evolutionary framework as Caro and Hauser (1992). They attempt to understand the mechanisms underpinning a form of teaching that they claim is unique to humans and that they name "natural pedagogy". Natural pedagogy requires *"(1) explicit manifestation of generalizable knowledge by an individual (the "teacher") and (2) interpretation of this manifestation in terms of knowledge content by another individual (the "learner")*" (Csibra & Gergely, 2006, p. 5). Hence, natural pedagogy is a form of teaching for a particular type of content: generalizable knowledge, such as rules, which can be applied to several contexts. According to Csibra and Gergely (2006, 2009, 2011), there are three requirements for pedagogy: ostensive signals (where the tutor has to reveal the fact that it is manifesting its knowledge, and therefore can be a costly behaviour), reference (the tutor needs to specify what information it is transmitting) and relevance (the tutor needs to recognise what knowledge is missing in the pupil, and impart that relevant knowledge). Moreover, Csibra and Gergely (2006) put emphasis on the cognitive mechanisms required in the pupil to make sure that it will benefit from the teaching. The pupil has to be receptive to pedagogy and receptive to opaque and generalizable information. For instance, they claim that children are sensitive to ostensive signals such as direct eye contact and infant-directed speech (Csibra & Gergely, 2006, 2009, 2011).

Like most other authors Csibra and Gergely (2006) do not assume that language is necessary for pedagogy, but unlike Tomasello and colleagues, (Tennie, Call, & Tomasello, 2009; Tomasello et al., 1993) they also do not assume that theory of mind or intentionality is necessary for pedagogy. Csibra and Gergely's (2006, 2009, 2011) definition is narrower than Caro and Hauser's

(1992) because the information transferred from the tutor to the pupil is generalizable rather than context dependent (Csibra & Gergely, 2011).

Contrarily to Tomasello and colleagues (Tennie et al., 2009; Tomasello et al., 1993), Csibra and Gergely (2006, 2009, 2011) also argue that pedagogy evolved as an adaptation during the course of human evolution, and that it arose before either language or the ability to attribute mental states. Csibra and Gergely (2006, 2009, 2011) define natural pedagogy as a uniquely human adaptation, crucial to culture. For them, human and non-human teaching are inherently different. This suggests that although they use a functional approach, natural pedagogy probably evolved to solve a different adaptive problem, than that found in non-human teaching contexts (Kline, 2015).

#### 1.1.3.2 Mentalistic approach

Regarding the mentalistic approach to teaching, no unique definition is used, but generally teaching is considered to be a behaviour where the tutor has the intention of facilitating learning in a pupil e.g.: "*when faced with the question of determining whether an action is a teaching action as opposed to some other action such as reciting, talking or acting in a play, it is the intention of bringing about learning that is the basis for distinguishing teaching from other activities. The intention the activity serves, then, is a part of the meaning of the concept, and not a factual discovery one makes about the activity*" (Pearson, 1989, p. 66). Here there is therefore a particular emphasis made on theory of mind, which, according to Tomasello et al. (1993) and Strauss et al. (2002) is a prerequisite for teaching. In fact, researchers have shown from an experimental study that changes in children's teaching strategies correlate with changes in success on theory of mind tasks supposedly alongside their understanding of the knowledge gap in the pupil (Strauss & Ziv, 2012; Strauss et al., 2002; Ziv & Frye, 2004). However, to my knowledge, it has never been shown empirically that theory of mind or the attribution of mental states is required to teach, in a functional sense. With the mentalistic approach, the tutor and sometimes the pupil, have to be aware of the intention of the tutor and of the knowledge gap between the

tutor and the pupil (Strauss & Ziv, 2009, 2012; Strauss et al., 2002; Tomasello et al., 1993; Ziv & Frye, 2004). Strauss et al. (Strauss, Calero, & Sigman, 2014; Strauss, Ziv, & Frye, 2015) also argue that teaching requires bidirectional communication between the pupil an the tutor, and, that similar to natural pedagogy, the knowledge or skills passed on are generalizable (Premack, 2007; Premack & Premack, 1996; Strauss & Ziv, 2012).

Because evidence of intent and attribution of mental states in non-human animals is limited, it is difficult to infer in non-human species, even among great apes. A definition of teaching that would require those capacities, would risk limiting this behaviour by definition to humans (Hoppitt et al., 2008; Thornton & Raihani, 2008), although there is some evidence for theory of mind precursors in animals (Bugnyar, Reber, & Buckner, 2016; Call & Tomasello, 2008).

#### 1.1.3.3 Cultural approach

Some authors claim that teaching is universal in human societies (Csibra & Gergely, 2009; Strauss & Ziv, 2012; Strauss et al., 2002). However, when looking at ethnographic work, authors disagree on what is considered to be teaching and its presence in different societies. In fact, some anthropologists consider that only Western culture teach because only a behaviour that resembles formal classroom teaching as seen in Western societies is considered teaching (see Kline, 2015, for review). Just like the mentalistic approach, in this cultural approach to teaching, the intent of the tutor is also important, but knowledge is always going from the tutor to the pupil and the pupil is passive (they do not interact with the teacher). Moreover, the "teaching activity" is also recognised as such by the participants (Kline, 2015). With this definition, teaching has also been reported in horticultural/farming societies but data on teaching in hunting and gathering societies remains controversial (see Strauss & Ziv, 2012). However, these reservations are related to direct instruction and there is evidence of more subtle forms of teaching. In fact, by using a functional definition, Hewlett et al. (2011) found evidence of teaching in the Aka and Bofi hunter-gatherer societies. Hewlett and Roulette (2015) further report regular

teaching events in the Aka hunter-gatherers. In the Aka societies' study, the most common forms of teaching were those categorised as natural pedagogy (Gergely & Csibra, 2006), negative feedback, and demonstration, while verbal explanations were more rare. Hewlett and Roulette (2015) found a significant correlation between natural pedagogy and imitation in the pupil, suggesting that natural pedagogy might play an important role in imitation. It is however unknown whether the pupils learned from the "taught" events.

In Hewlett and Roulette's (2015) study, many of the skills or knowledge transferred through teaching were easy to observe and fairly basic, a finding that challenges the conclusion of models such as the one presented in Fogarty et al. (2011) which suggest that teaching is limited to complex skills or limited to contexts where there are few alternative learning opportunities for observers. Using a functional approach, anthropologists describe different forms of teaching, but compared to other social learning process such as imitation, all forms of teaching are relatively rare in the Aka and Bofi hunter-gatherer communities studied (Hewlett et al., 2011). However, in a cross-cultural review of the anthropological literature Garfield et al. (2017) found that teaching was the most common social learning process observed in hunter-gatherer societies – more common than imitation or other forms of observational learning. Hence, when using a definition of teaching based on the functional approach, rather than a definition of teaching based on the Western-centric conception of teaching, there is abundant evidence that teaching is common in hunter-gatherer societies, and support for teaching to be regarded a natural human capacity (Strauss & Ziv, 2012).

## 1.2 Limitations of Caro and Hauser's (1992) definition

### 1.2.1 Teaching in humans versus non-human animals

Many of the issues and limitations raised concerning Caro and Hauser's (1992) definition come from fields other than animal behaviour. For instance, authors have questioned the value of this definition in understanding human teaching, particularly as some aspects of human teaching seem unique to our

species (Byrne & Rapaport, 2011; Fogarty, 2015). One problem with the definition is how to understand the cases of "failed teaching" where an individual could modify its behaviour to promote learning in another, but without succeeding in inducing learning (Frye & Ziv, 2005; Rapaport & Byrne, 2012). This problem does not arise in the mentalistic approach, as the intent to teach would be sufficient to categorise a behaviour pattern as teaching. But Caro and Hauser's (1992) definition would not consider those cases of failed teaching as teaching behaviour, because the definition assesses teaching based on outcomes, which would be non-existent in the cases of failed teaching.

### 1.2.2 Empirical limitations of the definition

On top of the aforementioned amendments to Caro and Hauser's (1992) operational definition, there are some empirical limitations in studying teaching, especially in the wild. For instance, the third criterion (pupil learning) can often only be assessed through experiments. However, experimental manipulation is not always possible or ethical depending on the species or behaviour investigated (Byrne & Rapaport, 2011; Fogarty, 2015; Hoppitt et al., 2008). Hence Fogarty (2015) suggests that the approach could be changed in order to identify learning through observation, without requiring experimental manipulation. For instance, if there is more success after a bout of teaching than a bout of observational social learning or asocial learning, this could be used as evidence that the individual is learning from teaching, and that teaching is more effective than any other sorts of learning, which would be crucial for the evolution of teaching (Fogarty, 2015). Similarly, Thornton and Raihani (2008) recommend examination of correlations between potential teaching behaviour and the pupil's success (Thornton & Raihani, 2008). This acknowledges that much of the time we might have to address the criteria with observational rather than experimental data. Zefferman (2016) puts forward another option: instead of attempting to detect teaching at an individual level (which has been the case until now), he suggests that teaching could be detected at a population level, by looking at the patterns of transfer of behaviour. For instance, Zefferman (2016) suggests that in species where there is uniparental care, and where information

or skills are transmitted from generation to generation with a sex-bias, this could be indicative of teaching behaviour. Examples Zefferman (2016) gives that could be indicative of teaching in hard-to-study species are sponging behaviour in dolphins (*Tursiops truncatus*), and nut-cracking and termite fishing in chimpanzees (*Pan troglodytes*), because they are sex-biased and uniparentally transmitted. However other explanations are consistent with this pattern. For instance, sex-biased transmission of information could be linked to sex-biased dispersal, where the sex to which the information is preferentially transferred to could be the sex that remains longer in the group, or to sex-biased social behaviour where the sex to which the information is preferentially transferred to is in more contact with the knowledgeable individuals.

It is also not always straightforward to measure the cost of a behaviour pattern (second criterion) as such costs could be immediate or have impacts on the long term. Thornton and Raihani (2010) categorise costs into four types: (1) costs associated with time lost where individuals could have been doing other things, (2) costs in terms of lost investment, (3) cost through the creation of a situation that could put both the tutor and pupil in danger, and (4) energetic costs. Energetic costs are very difficult to quantify directly, so proxies often have to be used, such as weight or size (Thornton & Raihani, 2010). One other way that Thornton and Raihani (2010) propose to assess the costs of potential teaching behaviour is to manipulate the costs directly. For instance, by reducing hunger and experimentally provisioning particular individuals, it would be expected that teaching efforts would increase. However, as noted above, such experimental manipulations are not always possible. Manipulating the cost of teaching, would also allow researchers to investigate whether the decision to teach varies based on its cost.

### 1.3 Classifications of teaching behaviour

Caro and Hauser's (1992) criteria allow for the detection of teaching behaviour, but not for the differentiation of different types of teaching behaviour. When Caro and Hauser (1992) proposed their definition, they also suggested

two categories under which teaching could be classified: "opportunity teaching", and "coaching". They define opportunity teaching as a "*situation conducive to acquiring a new skill or knowledge*" (p.166) and coaching as a behaviour where the tutor "*directly alters the behaviour of a [pupil] by encouragement or punishment*" (p.167). It is, however, not clear what evidence for teaching is required to decide between these two categories. Moreover, those categories do not allow for a further investigation of the different mechanisms that could be underpinning teaching in different species (Fogarty, 2015; Kline, 2015). In fact, the four non-human animal species that fulfil the three criteria of the Caro and Hauser (1992) definition of teaching, and which were reported after the creation of this definition, do not easily fall into those two categories (Hoppitt et al., 2008). In their original paper, Caro and Hauser (1992) suggested that as evidence of teaching in animals was discovered, their definition should be modified to fit the evidence. Hence, several categorisation schemes have been proposed in the following years based either on underlying social learning mechanisms, types of information transferred or adaptive problems teaching solves (function).

### 1.3.1 Classification of teaching based on social learning mechanisms: Hoppitt et al. (2008)

One categorisation was proposed by Hoppitt et al. (2008) who classify teaching based on the corresponding social learning mechanisms underpinning them. Rather than regarding teaching as additional mechanisms for the social transmission of information, they suggest that teaching can be viewed in parallel to other social learning processes. They argue for a separation of the learning process from the teaching process with social learning mechanisms relating to the processes observed in the pupil, and another layer added relating to the processes observed in the tutor. Hence the same social learning mechanisms could apply to teaching, with the difference being that when engaging in teaching, the demonstrator is not passive. According to Hoppitt et al.'s (2008) newer classification, teaching can happen through local enhancement, observational conditioning, imitation, opportunity providing, and coaching.

Teaching can therefore evolve alongside existing social learning processes. With this classification, human and non-human teaching might appear less distinct than was previously thought (Hoppitt et al., 2008). This classification is very useful to the study of teaching behaviour as it allows one to bridge the gap between the ultimate explanation of teaching (its function to promote learning) and the proximate explanations (the mechanisms that are involved in the behaviour).

Other authors such as Ewer (1969) and Thornton and Raihani (2010) have emphasised the learning aspect of teaching behaviour (outcome). This supports Hoppitt et al.'s (2008) classification rather than Kline's (2015) (explained in 1.3.3) where the emphasis is on the behaviour of the teacher.

### 1.3.2 Classification of teaching based on the type of information transmitted: Thornton and Raihani (2008)

As mentioned earlier (1.1.2.2) some authors suggest that teaching should only be considered for the transmission of non-declarative information (Leadbeater et al., 2006). Although Thornton and Raihani (2008) disagree with this, they propose that teaching could be classified based on the type of information transferred, while still considering active transmission of declarative knowledge as teaching. Hence they claim that "progressive teaching" could be favoured to transmit procedural knowledge, as the tutor has to adapt to the skill level of the pupil. This is more likely to evolve in species where there are extensive periods of parental care, when pupils have the time to acquire difficult-to-obtain skills (Thornton & Raihani, 2008). On the other hand, they coin "fixed teaching" to refer to the transmission of declarative knowledge. They call it "fixed" because the knowledge is binary: an individual has the knowledge/skill or not. Hence there is no need for the teaching to be progressive. Here the tutor will transmit just one specific piece of information and does not need to adapt to the knowledge of the pupil.

### 1.3.3 Teaching based on the adaptive problem it solves: Kline (2015)

Hoppitt et al.'s (2008) and Thornton and Raihani's (2008) classification schemes of teaching behaviour do not create distinct categories for forms of teaching that have only been observed in humans such as natural pedagogy as defined by Csibra and Gergely (2006, 2009, 2011). Other categories could be added to show aspects of teaching that require mental state attribution ["active teaching" (Caro & Hauser, 1992), "intentional teaching" (Byrne, 1995) and "instructive teaching" (Tomasello et al., 1993)]. Kline (2015) attempts to bridge the gap between teaching found in non-human animals and teaching that is supposedly unique to humans by classifying different types of teaching based on the adaptive problems that each type solves (compared to the mechanistic framework proposed by Hoppitt et al., 2008, or the framework based on the tutors' behaviour proposed by Caro & Hauser, 1992). She proposes the following teaching types: (1) "teaching by social tolerance", where the tolerance of the tutor towards the pupil is greater than usual [although Rapaport (2015) questions whether passive tolerance can really be considered teaching because this behaviour, in accordance with Hoppitt et al. (2008), probably did not evolve in order to promote learning in the pupil, and is initiated by the pupil rather than the tutor], (2) "teaching by opportunity provisioning", where the tutor creates an opportunity for the pupil to learn asocially, (3) "teaching by stimulus or local enhancement", where the initial interest of the pupil in a stimulus or location is stimulated by the tutor, (4) "teaching by evaluative feedback", where the tutor reinforces (positively or negatively) the behaviour of the pupil [also called coaching in Caro and Hauser's (1992) classification]. "Teaching by opportunity provisioning" (2), and "teaching by stimulus or local enhancement" (3) align with Hoppitt et al.'s (2008) scheme. Kline's (2015) final type of teaching is (5) "direct active teaching", which is similar to Csibra and Gergely's natural pedagogy, but without the ostensive signalling. This latest form of teaching requires that the tutor and pupil share the same background knowledge. According to Kline (2015), direct active teaching has currently only been found in humans, and this could be because of specific cognitive abilities in this species, or because humans are the only species in which direct active teaching would be adaptive. It could

also be because it is the only species in which we could gather evidence for this type of teaching. In this light, Tatone and Csibra (2015) argue that another category should be added to resolve the adaptive problem of acquiring opaque information, particularly in the context of human culture.

Kline's (2015) framework categorises teaching according to the learning problem that it solves, rather than an observable behaviour or the accepted social learning mechanism. However, similar to the functionalist definition, here theory of mind is not regarded as necessary for any of the categories of teaching. One problem with this classification based on solving the adaptive problem is that it does not necessarily match with the underlying mechanisms used, and therefore previous classification schemes, since more than one mechanism can solve the same adaptive problem, and more than one adaptive problem can be solved by the same underlying mechanism (Chouinard-Thuly & Reader, 2015). For instance, to solve the problem that "*a pupil attends to relevant stimuli, but does not have the knowledge or skill to undertake some task because it requires observing a conspecific's behaviour*" (Kline, 2015, p. 7), the pupil could learn through "imitation" or "observational conditioning" (mechanisms from Hoppitt et al., 2008). Moreover, Kline's categories are not mutually exclusive (Moore & Tennie, 2015). Kline's (2015) classification also emphasises evolved specialisations. Chouinard-Thuly and Reader (2015) argue that not all teaching rests on evolved traits, and strategies can be the result of previous experience and may be quite flexible (for instance, see: Kleindorfer, Hoi, et al., 2014; Lindeyer, Meaney, & Reader, 2013; Richardson et al., 2007). This has not been taken into account in Kline's (2015) framework. Hence this classification might not be the most useful when attempting cross-cultural and cross-species comparison of teaching behaviour. On the other hand, Kline's (2015) new framework is the first to attempt to bring different fields together, by incorporating direct active teaching, which has currently only been observed in humans (Rapaport, 2015).

### 1.3.4 Future directions for teaching classifications

Because teaching in humans is often studied differently than in other species, Kline (2015) suggests that a more systematic approach to studying teaching in humans is necessary, particularly in order to form a database of the different types of teaching she advocates. In addition to categorising species by whether they teach or not, the different classification schemes of teaching behaviour have allowed researchers to consider different nuances of teaching (1.3). What is still lacking from the research is the study of the different underlying cognitive mechanisms and neurobiology involved in teaching (Byrne & Rapaport, 2011; Rapaport, 2015; Rapaport & Byrne, 2012), as well as the ontogeny of the different teaching types (Beck, 2015; Palagi, Stanyon, & Demurua, 2015). There are some studies investigating the differences in teaching in children at different ages, but these are restricted to children from societies of industrialised countries (Strauss et al., 2002). Little is known about the development of teaching in non-human animals and in humans from non-industrialised societies (Strauss et al., 2015). An operational definition that applies both to human and non-human species and satisfies all fields is still missing (Eshchar & Fragaszy, 2015).

## 1.4 Conclusions on teaching definitions

Despite its limitations, Caro and Hauser's (1992) definition of teaching behaviour remains the most useful for my thesis. The aim of my thesis is primarily to investigate whether pupils learn from the putative teaching behaviour in three contexts. Those contexts are considered putative teaching cases, because there is evidence that individuals modify their behaviour in the presence of naïve conspecifics. However it is not known what the function of those modified behaviours are, and particularly whether those modified behaviours facilitate learning in the naïve conspecific. This corresponds to the third criterion of Caro and Hauser's (1992) definition. Using this definition allows me to investigate the function of those cases, without necessarily looking at the mechanisms involved. Because the aim of my thesis is to focus on the

function of the putative teaching cases, rather than the mechanisms by which teaching occurs, using Caro and Hauser's (1992) definition, instead of definitions in the mentalistic or cultural approaches, is necessary. In fact, both the mentalistic approach, and to a certain extent the cultural approach, to teaching, focus on the mechanisms by which learning is promoted. According to those approaches, the function of the behaviour, i.e. whether the behaviour results in learning, is less important. Hence by adopting Caro and Hauser's (1992) definition, I acknowledge that the function of teaching is to promote learning, but that many different mechanisms are possible to achieve this function (Thornton & Raihani, 2008). Caro and Hauser's (1992) definition also allows me to separate the learning aspect from other processes that are involved in teaching, as well as factors that are thought to be unique to humans. Moreover, because the definition is based on a functionalist approach, it allows me to experimentally test and measure behavioural differences to assess whether individuals socially learn from putative teaching contexts, rather than rely on unobservable cognitive processes.

## 1.5 Evolution of teaching behaviour

### 1.5.1 How teaching evolved and where to look for teaching behaviour

#### 1.5.1.1 Benefits

To meet functional definitions, teaching must come at a cost or no immediate benefit to the tutor, but teaching must benefit the tutor in the long term by increasing its inclusive fitness, for teaching to evolve in the first place (L. Castro & Toro, 2004; Galef, Whiskin, & Dewar, 2005; Kline, 2015; Thornton & Raihani, 2008). Benefits could take several forms. If teaching occurred between related individuals, then a benefit of teaching could occur through kin selection (Hoppitt et al., 2008) (1.5.1.4). If teaching occurs between parents and offspring, then further benefits could come in the form of earlier independence of juveniles meaning that parental investment does not have to last as long, and the parents could invest in their own survival or their future reproductive success (Thornton & Raihani, 2008). These benefits could also be key for unrelated helpers

engaging in teaching behaviour. These are not strict alternatives. Mancini and Palagi (2015) also compare the benefits of play and teaching and suggest that possible benefits could take place through the pupil becoming a future mate or ally to the tutor.

#### 1.5.1.2 Costs and opportunities

Because of the cost incurred by the tutor, if the pupil is likely to acquire the skill or knowledge easily from inadvertent social learning or asocial learning, either because there are a lot of opportunities to do so, or because the costs of learning from inadvertent social learning or asocial learning are low, then teaching is unlikely to be selected for (Fogarty et al., 2011; Thornton & Raihani, 2008). For instance, if pack hunting carnivores can learn to hunt by joining the pack, then the utility of teaching would be low. However, in solitary hunters, young do not have much opportunity to acquire the relevant knowledge or hunting skills, so teaching becomes more valuable (Fogarty et al., 2011; Thornton & Raihani, 2008). Hence it is expected that teaching could be common in solitary hunting species compared to group hunting species (Thornton & Raihani, 2010). Similar inferences can be made for the current absence of teaching in non-human great apes. In great apes, there are a lot of opportunities for juveniles to acquire information and skill through observation because of extended parental care. Hence teaching is unlikely to occur (Thornton & Raihani, 2010).

Theoretical models support these hypotheses. Mathematical models show that a genetic propensity for teaching is more likely to evolve when the behaviour transmitted is difficult to acquire independently or through inadvertent social learning (Fogarty et al., 2011). Fogarty et al. (2011) also found that when the trait is difficult to learn, and therefore few teachers possess the information to pass on, teaching is also unlikely to evolve. The information or skill transmitted through teaching has to be frequent enough in the population for tutors to possess this behaviour (L. Castro & Toro, 2014; Fogarty et al., 2011). Moreover, the fitness benefit of the target skill must be high for teaching to

evolve (Fogarty et al., 2011). Because there is a small range of contexts in which teaching is efficient, this could explain why it is not widespread in many animal species.

When modelling teaching as a socially transmitted trait rather than a genetically transmitted one, Nakahashi (2015) also found that teaching is more likely to evolve when the cost of social learning is low compared to that of individual learning. He further found that teaching is likely to evolve when social learning is accurate (in contrast to Fogarty et al., 2011), when the environment is stable and when the teaching has a large effect (Nakahashi, 2015).

#### 1.5.1.3 Social learning mechanisms

Learning resulting from the tutor's modified behaviour has to exceed the learning resulting from inadvertent social learning or asocial learning, which could also explain why teaching is quite rare. However, Hoppitt et al. (2008) suggest that teaching would evolve in the tutor only when "*the relevant social learning mechanism is already in place in the observer*" (p. 492). For instance, teaching with local enhancement will have arisen from inadvertent local enhancement, and therefore only the tutor would need to change its behaviour in a way to promote learning from local enhancement in the pupil. Hence species must have the capability for that form of social learning potentially expressed in many traits. When a new trait arises for which the social learning is either relatively ineffective or costly, or the inadvertent social learning opportunities are low, this could lead to the evolution of teaching of this trait. Mathematical models also show that when modelled as a socially transmitted cultural trait, the evolution of teaching becomes highly dependent on that of social learning (Nakahashi, 2015).

#### 1.5.1.4 Relatedness

Due to its costly nature, and according to Hamilton's rule (1964), it is expected that teaching should be favoured where potential tutors and pupils are closely related (Hoppitt et al., 2008). Hence, teaching could be more common

than expected as a form of parental investment, where species already invest a lot in the development of their offspring (Hoppitt et al., 2008; Thornton & Raihani, 2010; Thornton et al., 2007). In parent-offspring teaching, the cost of teaching should be less than half of the benefit to the young (Galef et al., 2005). Other systems where interacting individuals are highly related, such as social insects, are likely to favour the evolution of teaching (Fogarty et al., 2011; Franks & Richardson, 2006; Hoppitt et al., 2008; Leadbeater et al., 2006; Thornton & McAuliffe, 2006). Finally it is expected that teaching might be more common in cooperatively breeding species, partly because helpers are usually related to the parents and offspring (Kline, 2015) (1.5.1.5). However the benefits of teaching for the tutor and the pupil are probably different due to the relatedness between the tutor and pupil and the impact that the learning has on the survival and reproductive success of the pupil (Kleindorfer, Hoi, et al., 2014).

Fogarty et al. (2011), through theoretical modelling, also found that teaching, like other altruistic behaviour, is more likely to evolve to be directed towards related individuals, but only if the behaviour taught is sufficiently difficult to acquire that it is unlikely to be picked up by other means. Moreover, Nakahashi (2015) suggests that teaching offspring is a pre-adaptation to teaching individuals that are not related.

#### 1.5.1.5 Cooperative breeding systems

Teaching, being a costly behaviour that benefits others, is also a type of altruism (Fogarty et al., 2011; Hoppitt et al., 2008; Thornton & Raihani, 2010), and presupposes cooperative motives (Thornton & McAuliffe, 2012). Given this, Kline (2015) suggests that species more likely to have evolved teaching might be cooperatively breeding species or species with already high parental investment. In fact, candidate cases of teaching seem to come predominantly from cooperatively breeding species. The indirect fitness benefits associated with the high levels of relatedness between helpers and young in cooperative breeding species may increase the probability of the evolution of teaching in these species (Bourke, 1997; Emlen, 1991; Thornton, 2008). Hoppitt et al. (2008) suggest that

this could be because either cooperative breeding promotes teaching (high relatedness, investment in offspring) or because an external factor, such as the high cost of rearing, selects for both cooperative breeding and teaching. In fact, cooperative breeders are already engaged in costly care of the young, and teaching could reduce their time investments. Moreover, the cost of teaching is shared between multiple individuals in cooperative breeding societies, making teaching for each individual more economical (Fogarty et al., 2011; Thornton, 2008). It is also possible that cooperatively breeding species are easier to study (perhaps because of bigger group size, compared to parent-infant-only groups, makes them easier to observe), and therefore teaching is easier to detect in those species.

### 1.5.2 Theories on the evolution of teaching in humans

#### 1.5.2.1 Cumulative culture

Researchers using modelling techniques have also attempted to explain the particulars of the evolution of teaching specifically in humans, rather than in every species. Teaching, alongside imitation, is often thought to be a major process in the development of human culture (Boesch, 1991; Boyd & Richerson, 1985; Csibra & Gergely, 2006; Nakahashi, 2015), particularly because of the rarity of teaching in non-human species and the prevalence of this behaviour in humans. Tomasello et al. (Tennie et al., 2009; Tomasello, 1994; Tomasello et al., 1993) suggest that teaching (and imitation) are crucial to the evolution of cumulative culture, an aspect of culture that has currently only been observed in humans (Boyd & Richerson, 1996; Csibra & Gergely, 2011; Galef, 1992; Tennie et al., 2009; Tomasello et al., 1993; Whiten, 2011). Recent experimental evidence comparing capuchins (*Sapajus apella*), chimpanzees and children (Dean, Kendal, Schapiro, Thierry, & Laland, 2012) as well as theoretical modelling (L. Castro & Toro, 2014; Fogarty et al., 2011) seem to support those claims. In fact, Fogarty et al. (2011) also found that in humans, teaching [or direct active teaching in Kline's (2015) terminology] could have evolved because cumulative culture allows for difficult-to-acquire traits to be available in the population. Moreover, Castro and Toro (2004) stipulate that imitation was necessary, but not sufficient, for

cumulative culture to evolve in humans compared to other primates, but that teaching played crucial role by making learning less costly and more accurate. However, Castro and Toro (2014) propose that teaching is necessary for the transmission of complex behaviour observed in human cumulative culture. Hence, according to Castro and Toro (2014) for cumulative cultural transmission of complex behaviour as seen in humans, a high fidelity mechanism, such as teaching, is necessary. It is not certain which - teaching or cumulative culture - promoted the evolution of the other and Fogarty et al. (2011) stipulates that they could have coevolved.

Many claim that high fidelity copying is essential to cumulative culture, and that teaching is an important mechanism for high fidelity copying. Zwirner and Thornton (2015) showed in a chain experiment where humans had to make efficient baskets, that individuals using teaching made more robust baskets, but teaching was not necessary to human cumulative culture. This is inconsistent with teaching being necessary for cumulative culture. Similar findings were reported by Caldwell and Millen (2009). Morgan et al. (2015) also found greater improvements in flint knapping when using teaching (particularly verbal teaching) relative to reverse engineering, but all conditions did show improvement, whether teaching was present of not. However, Morgan et al.'s (2015) findings that verbal teaching increases the performance of flint knapping compared to gestural teaching suggests that language in combination with teaching increased the fidelity of copying thus allowing for the cumulative culture observed in humans. Hence experimental evidence questions whether teaching is necessary for high fidelity copying, but generally supports the notion that it promotes higher fidelity copying than is possible in its absence.

#### 1.5.2.2 Evolution in *Homo*

Compared to teaching in non-human animals, teaching in humans commonly occurs between unrelated individuals (Nakahashi, 2015). This, in addition to the absence of evidence of teaching in chimpanzees, suggests that humans' reliance on teaching probably evolved after human and *Pan* became

different lineages (Nakahashi, 2015). Moreover, because different societies take part in very different forms of teaching, Nakahashi (2015) suggests that teaching behaviour could be culturally transmitted. However, many other authors claim that teaching is universal to humans (although this is not accepted by all anthropologists), and that infants do not need to be taught how to teach (Csibra, 2007; Csibra & Gergely, 2009, 2011).

Csibra and Gergely hypothesise that natural pedagogy first evolved in the context of tool use and tool creation, because the goals of tool making can be opaque (Csibra & Gergely, 2006). Without pedagogy, it would be much harder to acquire this opaque information with other social learning forms (Csibra & Gergely, 2009; see also Morgan et al., 2015). According to them, natural pedagogy would then have generalised to other domains. Csibra and Gergely (Csibra, 2007; Csibra & Gergely, 2006, 2009, 2011) also claim that one of the main differences between human and non-human teaching is the type of information transferred: humans usually transfer generalizable information, while non-human animals transfer context dependent information (but see teaching in meerkats, Thornton & McAuliffe, 2006). On the other hand, Premack (2007) argues that human and non-human animals' teaching is very different because while non-human animal teaching is an adaptation to fulfil a single evolutionary problem - a single target - he claims that human teaching is not an adaptation, but a domain general competence that can be used on many targets.

### 1.5.3 Concluding remarks on the study of the evolution of teaching

Research on the evolution of teaching has emphasised studying the costs and benefits of this behaviour, similar to the evolution of altruism. However, when the research focuses on human teaching, emphasis is put on the links between teaching and cognitive mechanisms unique to humans, while research focusing on the evolution of teaching in non-human animals has concentrated on the socio-environmental factors that favour teaching. Several authors suggests focusing on socio-environmental factors to investigate where different teaching types might evolve, rather than focusing on the psychological prerequisites

(Hoppitt et al., 2008; Kline, 2015). Species most likely to exhibit teaching are therefore cooperative breeders, solitary hunters of relatively larger or dangerous prey, and species in which the relevant form of social learning is already present (Hoppitt et al., 2008; Kline, 2015; Rapaport, 2006).

## 1.6 Experimental evidence of teaching in non-human animals

In my judgement, there are only four species that have been found to fulfil all three of Caro and Hauser's (1992) criteria in the wild: tandem-running ants (Franks & Richardson, 2006), meerkats (Thornton & McAuliffe, 2006), pied babblers (*Turdoides bicolor*) (Raihani & Ridley, 2008) and superb fairy-wrens (*Malurus cyaneus*) (Colombelli-Négrel et al., 2012). A common feature of all four species is that they live in cooperative societies, where individual investment in teaching could be relatively low because of shared costs (Hoppitt et al., 2008). Below I present the evidence for teaching in these species, before going on to consider some other possible cases.

### 1.6.1 Tandem-running ants

The ants *Temnothorax albipennis* live in colonies, and need to transmit information about nest sites and food sources efficiently to their nest mates. They can explore the territory solitarily, but can also do so in pairs or groups. For instance, once they have a good location, they can carry nest-mates on their back to bring them to the new locations, or they can also use tandem-running. During tandem-running, knowledgeable individuals will travel towards the new nest site or food location accompanied by a naïve follower, but only when tapped frequently on the abdomen by the follower's antennae (Franks & Richardson, 2006). Franks and Richardson (2006) claim this is a case of teaching which functions to make the naïve follower learn the route to the food source, so that in turn they can recruit more nest-mates to the new location. This satisfies Caro and Hauser's (1992) first criterion, as tandem-running ants only do this in the early stage of migration towards a new location. Later in the migration tandem-running ants switch to nest-mate carrying, which is three times faster than tandem-running, but does not allow the naïve individual to learn, and therefore

recruit other ants (Pratt, Mallon, Sumpter, & Franks, 2004). Moreover, tandem-running makes ants take four times as long to get to the new location compared to when they travel alone (Franks & Richardson, 2006). This satisfies Caro and Hauser's (1992) second criterion. Although it slows down the leader, tandem-running enables the follower to learn the route faster than it would have on its own, satisfying Caro and Hauser's (1992) third criterion.

This teaching behaviour can be applied to a context other than foraging since tandem-running in ants is also used to establish new colonies, and explore territory (Aron, Pasteels, Deneubourg, & Boeve, 1986; Duncan & Crewe, 1994; Richardson et al., 2007). In fact, the experiments in Richardson et al. (2007) were conducted during colony emigration. However, the third criterion of teaching has not been directly tested in all of these contexts. It is also the only case so far of non-human teaching where feedback has been demonstrated between the tutor and pupil. Ants evaluate the progress of their follower and have been shown to adjust their behaviour accordingly (Richardson et al., 2007). Through experimental work, Richardson et al. (2007) showed that tandem-running ants perform three different kinds of evaluations: (1) the more a leader has invested in the run, the longer it will wait for the follower to re-establish contact, (2) the higher the value of the goal, the longer the leader will wait for the follower to re-establish contact, and (3) the leader will stop waiting for the follower for a shorter amount of time if the run has been unusually slow. This shows that the leader not only teaches the follower the route, but the tutor is also sensitive to the competence or skill of the pupil and adapts it teaching behaviour accordingly.

Based on Hoppitt et al.'s (2008) classification, teaching in tandem-running ants can be viewed as teaching through local enhancement, where the tutor leads the pupil to the food source while adapting its pace to ensure that it is being followed by the pupil (Franks & Richardson, 2006).

### 1.6.2 Meerkats

Meerkats are cooperative breeders where every individual in the group helps raising the young, and teaches them how to correctly manipulate dangerous prey for foraging purposes. In meerkat societies, helpers bring back dead scorpions to young pups, disabled but live scorpions to slightly older pups, and intact live scorpions to the oldest pups (first criterion of the definition) (Thornton & McAuliffe, 2006). Thornton and McAuliffe (2006) found few costs to the tutor in modifying the prey itself, but found that tutors incurred costs once the prey was transferred. When feeding pups live prey rather than dead ones, tutors spent more time monitoring the pups handling the prey, pupils had higher risk of losing the prey and tutors had to invest more time and energy in retrieving prey items lost by pups and further modifying them (second criterion). Moreover, helpers that are still investing in their own growth are less likely to transfer live scorpions to the young, than older helpers are, further showing the cost of the behaviour (Thornton, 2008). Through experimental manipulation, when given extra opportunities to manipulate disabled prey, pups out-performed those that were only given dead scorpions. Hence, having the opportunity to handle live prey is beneficial to the pups' skill acquisition (third criterion) (Thornton & McAuliffe, 2006). Handing over prey items in different forms allows the pups to gradually learn to handle the prey items (Thornton & McAuliffe, 2006).

Since helpers provide the young with either dead, disabled or intact scorpions according to the age of the young (defined by the sound of their call), teaching in meerkats could be defined as opportunity teaching as helpers provide the opportunity for young to learn to process prey (Hoppitt et al., 2008; Thornton & McAuliffe, 2006).

### 1.6.3 Pied babblers

Pied babblers are also cooperative breeders, and adults will feed the young until they fledge. Adults pied babblers often give specific "purr" calls when they present nestlings with food, and they teach the young to associate those calls with food delivery (Raihani & Ridley, 2008). When juveniles fledge, adults then use purr calls to recruit fledglings and fledglings respond by approaching calling adults (Radford & Ridley, 2006; Raihani & Ridley, 2007). Juveniles benefited from this response as they received more food on arrival at the new location compared to when they were left behind and they also gain access to highly desirable food (Radford & Ridley, 2006; Raihani & Ridley, 2007). Fledglings also likely avoided predators by following adults away from the original location (Raihani & Ridley, 2007).

Calls are only emitted when offspring are present (Raihani & Ridley, 2008), adults only start emitting those calls 4-5 days before the offspring fledge, and the young respond only in their last day prior to fledge (first criterion) (Raihani & Ridley, 2007). This call does not increase the efficiency of feeding bouts: the calls are only used a few days before fledgling and purr calls do not always elicit begging, hence providing no direct benefit to the adult. Moreover, frequent purr calling was associated with weight loss in adults (second criterion) (Raihani & Ridley, 2008). Naïve nestlings initially do not respond to purr calls but their responses increase with age/experience. Offspring learn to associate purr calls with food delivery: nestlings beg in response to those calls (third criterion) (Raihani & Ridley, 2007). Moreover, hungrier fledglings respond faster than satiated ones, suggesting that the offspring couple the call with food delivery (Raihani & Ridley, 2007).

In contrast to the first two examples, teaching in pied babblers could be defined as teaching through observational conditioning, where the tutor actively exposes the pupil to a relationship between different stimuli: food provisioning and purr calls (Hoppitt et al., 2008).

### 1.6.4 Superb fairy-wrens

More recently, superb fairy-wrens have been found to teach their embryos "vocal passwords", that, upon hatching, allow the parents to discriminate their young from Horsfield's bronze-cuckoo parasite juveniles (*Chalcites basalis*) (Colombelli-Négrel et al., 2012). Mothers emit incubation calls that contain signature elements when embryos are in the late stage of incubation (first criterion). However those incubation calls are costly: nest predation is higher at nests that have higher incubation call rates (shown from both observational and experimental data) (second criterion) (Kleindorfer, Hoi, et al., 2014). This cost explains the variation in teaching observed in the population as the benefits of teaching are a trade-off to increased predation risks (Kleindorfer, Hoi, et al., 2014). Cross-fostering experiments show that embryos learn the signature element in the egg from their foster mother, and upon hatching, nestlings reproduce the signature elements of their mothers in their begging calls (third criterion). The more incubation calls the embryo hears, the more similar its begging call is to the signature vocalisation (Colombelli-Négrel et al., 2012; Kleindorfer, Evans, & Colombelli-Négrel, 2014). From a playback experiment, Colombelli-Négrel et al. (2012) showed that adults respond more to calls that include their signature elements compared to calls that did not. In particular, offspring that include the signature vocalisations in their begging calls receive more food than those that do not, and adults that hear their signature vocalisation spend less time being vigilant than those who do not. Mothers' specific calls shape offspring call similarity, which allows them to detect intrusions from parasitic cuckoo nestlings (Colombelli-Négrel et al., 2012). This is, so far, the only pre-natal teaching behaviour observed in non-human animals.

The series of experiments in superb fairy-wrens also show that individuals modify their investment in teaching according to environmental conditions (Kleindorfer, Evans, et al., 2014). In fact, because of the cost of teaching in this species (increased predation rate), Kleindorfer et al. (2014) predicted that teaching should (1) be lower in high predation areas but (2) higher in high brood parasitism areas. Where both predation and parasitism

risks are high, this should result in evolutionary adaptations towards making teaching more efficient where incubation calls have a higher signature call rates (Kleindorfer, Hoi, et al., 2014). When broadcasting playbacks of cuckoo songs near nests, females increased their incubation call rate (Kleindorfer, Evans, et al., 2014). This in turn increased the similarity between the mother's incubation call that included the signature calls and the nestlings' begging calls (Kleindorfer, Evans, et al., 2014). Cuckoo vocalisations are therefore sufficient for superb fairy-wrens to perceive the threat of brood parasitism and adjust their likelihood of detecting intrusion accordingly. If they are aware, from acoustic cues, that brood parasites are in the area, they will increase their effort in teaching behaviour, despite the cost, in order to increase their chances of detecting parasites in their nest (Kleindorfer, Evans, et al., 2014). Moreover, in this species, teaching has important evolutionary consequences as it could give advantage to the superb fairy-wren in the host-brood parasite arms race.

Based on Hoppitt et al.'s (2008) classification, this example could be considered teaching through vocal imitation, since the outcome (vocal password) of the tutor is reproduced by the pupil.

## 1.7 Suggestive evidence of teaching in non-human animals

In the following section, although I refer to the first, second and third criterion of Caro and Hauser's (1992) definition, I do not imply that there is strong evidence that each criterion has been met. I mention them only so that each aspect of the behaviour can be related to the definition. This section excludes the three cases on which my thesis is based as they are mentioned in the next section of this chapter (1.9) and explained in more details in Chapters 5, 6 and 7.

### 1.7.1 Mammals

#### 1.7.1.1 Carnivores

##### *1.7.1.1.1 Cheetahs*

When cubs are very young, mother cheetahs (*Acinonyx jubatus*) bring back live prey and kill it in front of the cubs. As the cubs grow, the mother instead releases prey in front of them for the cubs to hunt (first criterion). This could potentially teach them hunting skills (Caro, 1995). Bringing back live prey to cubs delays the mother from feeding, and it also means that they occasionally lose their prey (second criterion) (Caro & Hauser, 1992). Moreover, hungry mothers, assessed by the size of their belly, are less likely to release prey to their offspring, compared to satiated mothers. This suggests that there are energetic costs involved in the putative teaching behaviour (Caro, 1994). Caro (1995) found that the frequency of stalking and crouching during play in cubs was correlated with those behavioural patterns during hunting, and that individuals more involved in play behaviour contacted prey at higher rates when they were released by the mother, suggesting that individuals that stalk and crouch more during play may become better hunters. It could be possible that the release of live prey from the mother to her cubs provides cubs the opportunity to practise their stalking and crouching techniques, and increase their hunting success rate. However there is yet no direct evidence that the development of hunting skills is accelerated by mothers releasing live prey to their young (Caro & Hauser, 1992). Cubs' predatory skills improve during the period where mothers release prey, but it is not known whether it is a direct result of the mothers' behaviour or if it is a result of age (third criterion) (Caro & Hauser, 1992). Hence, evidence for learning is still lacking in this case.

##### *1.7.1.1.2 Domestic cats*

The potential teaching behaviour of cats (*Felis catus*) was observed by Ewer (1969) and then followed by experimental manipulations in Caro's (1980b) study. Ewer (1969), among others, described how mothers bring back live prey

to their offspring, and recapture it if it escapes. First, mothers bring prey and eat it in the presence of their kittens. Then they bring back dead prey without eating it; and later in life they bring live prey for the kittens to manipulate (first criterion). Moreover, when the kittens are young, mothers interact with the prey more if their offspring have not interacted with it for some time, but when kittens were interacting with prey they did not interrupt them (Caro, 1980b). Hence mothers seem to direct their kitten's attention towards the prey, and female cats also emit calls during foraging behaviour, which could potentially encourage kittens to interact with the prey (Ewer, 1969). With increasing age and skill of the kittens, mothers slowly inhibit their foraging behaviour to let juveniles interact with the prey. As kittens become more proficient hunters, mothers become less and less involved in catching the prey (Caro, 1980b; Ewer, 1969). Mothers also increase their latency to kill the prey when kittens pay more attention and interact more with the prey (Caro, 1980b). Cats without offspring do not in engage in this behaviour.

Caro (1980b) showed that the mother's behaviour affects kittens' hunting skills, and that the kittens' hunting behaviour also changes with age (Caro, 1981). Kittens increase their interaction with prey, killing and eating of the prey, when after having brought back the prey, mothers spent less time with it (third criterion) (Caro, 1980b). This is consistent with opportunity provisioning. However, further research showed that experience with a particular prey type only has a long term effect on interaction with that prey type, and not general hunting skills (Caro, 1980c). Hence it could be expected that the effect of the mother's behaviour similarly only influence their kittens on particular prey types rather than overall hunting skills.

Mothers also have a general effect on offspring behaviour. When exposed to prey in the presence of their mothers, kittens increase their rate of killing and predatory behaviour, and this is still observable when the kittens are adult (Caro, 1980a, 1981). Moreover, when mothers are present, motor patterns related to hunting are more frequent than when the mother is absent (Caro, 1980b). The presence of the mother during development has long-term effects on the

predatory skills of the kittens, potentially because they provide opportunities for kittens to practise their hunting skills by bringing them prey.

Regarding cats, there is no evidence yet evaluating the cost of the mothers' behaviour (second criterion). It can however be hypothesised that the costs are likely to be similar than the costs occurred by mother cheetahs, since their behaviour appear similar in mechanisms and adaptive value.

*1.7.1.1.3 Others*

Similar behaviour to the mother cats' and cheetahs' behaviour has been observed in tigers (*Panthera tigris*) (Schaller, 1967) and river otters (*Lontra canadensis*) (Liers, 1951), but to my knowledge, no experimental studies have been conducted to assess whether those behaviour fulfil Caro and Hauser's (1992) criteria.

1.7.1.2 Rodents (rats)

In a study with captive rats (*Rattus norvegicus*), Galef et al. (2005) devised an experimental paradigm that could test for teaching behaviour in a foraging context. However, these authors found no evidence that dams modified their behaviour to teach juveniles what food was good to eat and what food was toxic (first criterion). This is somewhat unsurprising as rats use other non-costly social learning means to learn about food palatability and pups can easily acquire information through asocial learning and other forms of social learning (Thornton & Raihani, 2008). In fact, in the same experiment, Galef et al. (2005) found that despite dams not modifying their behaviour, the pups preferred the food that the mother ate compared to the one she did not (third criterion).

1.7.1.3 Proboscidea (elephants)

Some female African elephants (*Loxodonta africana*) have been found to simulate oestrus (first criterion). One hypothesis of the reason for this behaviour is that they potentially teach younger females how to behave when they are in

oestrus. In fact, females simulate oestrus disproportionately when other females are experiencing oestrus for the first time, but it is not the only context in which they simulate it (L. A. Bates et al., 2010). Hence there could be other reasons for this behaviour other than to teach naïve females. Here, there is no empirical evidence satisfying the first, second or third criterion of Caro and Hauser's (1992) definition.

#### 1.7.1.4 Cetaceans

##### *1.7.1.4.1 Killer whales*

Observations of killer whales (*Orcinus orca*) in Patagonia suggest that males might teach juveniles how to hunt sea lions and elephant seals through intentional stranding (Lopez & Lopez, 1985). Lopez and Lopez (1985) describe six occasions where an adult and juvenile stranded themselves together (less than 4m apart) and captured prey independently. When juveniles had not caught their own prey, the adult would fling the prey it had caught towards the juvenile, who would then interact with it (first criterion). Moreover, they also report that in 41% of the instances where a juvenile was beached, the adult charged in the direction of the beach and the juvenile repeatedly. This seemed to encourage the juvenile to also repeat the beaching behaviour. These interactions between adults and juveniles made the authors consider the possibility of adults teaching their young how to hunt. Guinet and Bouvier (1995) further support the idea of teaching in killer whales from the Crozet Islands with the description of the development of two calves' stranding skills and the interaction with their mother. In this study, the calf that was the first to catch prey independently through the stranding technique was the one that was more involved in "beach play" (stranding with other individuals on beaches where no prey is present) with its mother, which is suggestive of social learning (third criterion) (Guinet & Bouvier, 1995). Moreover, adults were more successful hunters in the absence of juveniles, suggesting that the presence of juveniles while hunting is costly (second criterion) (Hoelzel, 1991). Teaching in killer whales is supported by the idea that long periods of time are required to acquire those hunting skills because of their "*technical difficulties*" (p. 32) and risk. Furthermore, Guinet and

Bouvier (1995) suggested that the long developmental period and the low reproductive turnover observed in the population could be related to the cost of parental investment. Teaching could potentially help shorten the developmental period, however, there is yet no evidence satisfying the second or third criterion of Caro and Hauser's (1992) definition.

#### *1.7.1.4.2 Atlantic spotted dolphins*

Another cetacean may teach their young hunting skills: Atlantic spotted dolphins (*Stenella frontalis*). Bender et al. (2009) have observed nine Atlantic spotted dolphin mothers chasing prey for significantly longer and making significantly more body-orientated movements in the direction of the prey when their calves were present than when they were not (first criterion). From a descriptive point of view, they found that when calves were present, mothers seemed to "*toy with their prey, making it more like play behaviour and less like typical foraging behaviour of mothers*" (Bender et al., 2009, p. 49), which is similar to the reports of potential teaching in killer whales and cats (Caro & Hauser, 1992; Guinet & Bouvier, 1995). Mothers seemed to provide the opportunity for their calves to observe hunting behaviour, and occasionally also gave them the opportunity to practice the necessary skills. Mothers were however never observed losing the prey when they altered their behaviour, but the increased chase time could also mean a decrease in opportunity to chase other prey (second criterion). It is however still unknown whether this behaviour has any effect on the calves' foraging skills (third criterion).

### 1.7.1.5 Primates

#### *1.7.1.5.1 Chimpanzees*

In 1991, Boesch described several instances where mother chimpanzees influenced their infants' attempts to crack nuts, that in Kline's (2015) terminology could be described as teaching though stimulus enhancement. Four mothers were witnessed to leave hammers or nuts near the anvil, where the young were. This was never observed when there was no infant (first criterion)

(Boesch, 1991). Because it takes a very long time for infants to acquire the necessary technique to open nuts, it would have been more efficient for the mother to crack open a nut for her infant, if the purpose of the behaviour was to feed the young. The mothers' behaviour decreases their foraging efficiency because the mothers need to find new tools and resources while the infants are using theirs (Boesch, 1991). Moreover, the behaviour comes at the cost of potentially losing the tools to another chimp (second criterion). There are two other instances where mothers were seen potentially teaching their young, which could be an example of " direct active teaching" (Kline, 2015). The first one was when "*the mother demonstrated the correct positioning of the nut, although the infant may well have succeeded in opening it independently eventually*" and the second when "*the mother corrected an error in her daughter's behaviour and Nina [the daughter] seemingly understood this perfectly, since she continued to maintain the grip demonstrated to her*" (p. 531-532) (first criterion). Although the infants were more proficient following the mother's adjustment, it is not known if they actually learned the technique and would reproduce the same grip without the mother present (third criterion). Nor is it known whether the tools were left in order for the youngsters to learn.

This example of putative teaching in chimpanzees is anecdotal, based on qualitative rather than quantitative data (as in elephants and killer whales). Boesch's (1991) descriptions of the observed behaviour rely heavily on attributed mental states [e.g.: "*they seem to have the ability to compare their offspring's behaviour to their own conception of how it should be performed and anticipate the possible effects of their action on those of their offspring*" (p. 532)]. Moreover, behaviour resembling teaching was only described once in wild chimpanzees, despite their having been studied for more than 60 years, which questions the interpretations of Boesch's (1991) findings. Minimally it implies that teaching is not a common form of transmission of information in this species. The absence of conclusive evidence of teaching in this species could be explained by the fact that other forms of social learning were sufficient to transmit relevant information about tools (Fogarty et al., 2011; Moore & Tennie, 2015), similar to what was found in rats.

In captivity, there is also a report of an individual who had been taught human sign language, moulding the hands of another individual, potentially influencing that individual's signing performance (Fouts, Hirsch, & Fouts, 1982). However, whether this came at a cost, or whether the naïve individual learned is not known.

More recently Musgrave et al. (2016) have claimed that chimpanzees teach through tool transfers. Change of possession of termite fishing probes from one individual to another were observed in Nouabale-Ndoki National Park (first criterion). Tool donors spent less time using probes, performed fewer fishing probe insertions, and fed less after having transferred their tool to another individual (second criterion). On the other hand, recipient of tools spent more time using probes, increased the number of probe insertions and fed more, after being transferred a tool, than before being transferred one (third criterion). However, all transfers were initiated by recipients, and not all recipients were naïve juveniles. Hence in this context, the transfer of tools does not satisfy the first criterion of Caro and Hauser's (1992) definition, as the authors provide no evidence that the putative tutor modifies its behaviour in any way. If the tool donor transferred tools only to naïve individuals, or transferred particular types of tools, for instance tools with a specific shape, length or material, that have been shown to be more efficient in termite extraction, then this could have been evidence supporting the first criterion of Caro and Hauser's (1992) definition. Evidence for the second criterion of Caro and Hauser's (1992) definition is more convincing as donors are less efficient at feeding on termites after losing their tool due to a transfer. On the other hand, I do not think that there is convincing evidence that the recipient of the tool learns as a consequence of the tool transfer. In fact, the recipient of tools could be more efficient at extracting termites after a tool transfer not because they have been given a tool, but simply because they have a tool in their hands that allows them to do so. An adequate control to show learning would have been to compare the foraging effort and success of recipient individuals after a tool transfer and the foraging effort and success of individuals after they acquired a tool on their own. Moreover, it would have been interesting to see the long-term effect of those transfers: are

individuals who receive more tools from transfers more efficient at extracting termites not directly after they have received a tool, but days or months after transfer events, compared to individuals that receive fewer tools as they grow up?

#### *1.7.1.5.2 Rhesus macaques*

There are reports of mother macaques (*Macaca mulatta*) moving away from their young and giving them signals to make the young come toward them, potentially to teach them motor skills. Some mothers were found to break contact with their infant prior to the infant breaking contact with them. When contact between the mother and her offspring was first broken, pairs where the mother broke the contact had younger infants, than pairs where the infant broke the bond (first criterion) (Maestripieri, 1995). They also found that breaking contact earlier correlated with a higher rate of kidnapping of the infants (Maestripieri, 1995). Kidnapping can vary a lot in terms of time the infant is separated from its mother, but it has been known to occasionally lead to the infants' death from starvation and dehydration (second criterion) (Maestripieri, 1993). Moreover, when kidnapping does not happen, mothers and infants are not separated for more than 30 seconds, which does not enable the mother to partake in any other beneficial activity (Maestripieri, 1995). Mothers who broke contact with their infant earlier in life had infants that broke contact from them earlier in life, compared to infants that were not left by their mothers. This suggests that mothers breaking contact can lead to developmental changes in the young, and potentially lead to infants being independent from them in terms of locomotion, earlier in life (third criterion) (Maestripieri, 1995). However, more experimental evidence is required before concluding that this is the case, because mother breaking contact with their infant earlier in life could also reflect differences in infant maturation (Maestripieri, 1995). Moreover, these data were obtained from captive groups of macaques, and it remains to be determined whether this behaviour occurs in the wild.

#### *1.7.1.5.3 Gorillas*

Similar to macaques, Maestripieri et al. (2002) report instances in gorillas (*Gorilla gorilla*) where mothers could be teaching their young how to navigate through their environment. There were clear reports of encouragement in the context of locomotion, and one observation of active provisioning (first criterion). Younger infants were encouraged more than older ones, but encouragement was still rarely observed compared to other behaviour, particularly behaviour where infants actively request mothers to participate in their activity or where infants observe their mothers without the mother actively modifying its behaviour. There is also no evidence of a cost of this behaviour (although it could be hypothesised that it is similar to that of macaques) or that the juveniles learn from it (second and third criteria).

### 1.7.1.6 Chiroptera (bats)

In a recent study, it has been shown that common big-eared bat mothers (*Micronycteris microtis*) transfer prey to their pups (Geipel, Kalko, Wallmeyer, & Knörnschild, 2013). 50% of the prey captured by mothers were transferred to their young. In 14.2% of those transfers, prey items were partially consumed by the mother before being transferred (first criterion), potentially to render the prey handling easier for the pup. The consumption of prey by the mother prior to transfer decreases over time, potentially because pups have gained experience as they matured (third criterion). However, when observing the prey consumption behaviour of the pups, Geipel et al. (2013) found that when consuming large prey they heavily relied on their wings. Mothers on the other hand rarely used their wings during prey consumption, suggesting that pups have not increased their prey handling skills, at least during the scope of this paper. The cost of prey transfer from mother to pups (second criterion) was not investigated.

### 1.7.2 Birds

#### 1.7.2.1 Florida scrub jays

In an experiment investigating social learning of free-living Florida scrub-jays (*Aphelocoma coerulescens*) in a foraging context, Midford et al. (2000) report three instances of potential teaching behaviour in two groups. Adults had to retrieve food hidden in locations marked with rings. In those three cases, instead of taking the food once it was uncovered, the adult "*either departed or stood over the depression it dug, pointed its bill downwards towards the pieces, until the juvenile took them*" (p. 1206). This behaviour was very different from the usual behaviour of adult birds once they had uncovered food (first criterion). From those three cases, Midford et al. (2000) did not see an improvement in foraging in the young having obtained food following the adult's modified behaviour (third criterion) but more active demonstrations might have been necessary to observe a change in the young's behaviour. Because this was an anecdotal report, there was also no evaluation of the potential cost of this behaviour (second criterion).

#### 1.7.2.2 White-tailed ptarmigans

Evidence supporting teaching behaviour in white-tailed ptarmigans (*Lagopus leucura*) is explained in Chapter 7 (7.2.1.1).

#### 1.7.2.3 Osprey

There are also reports that osprey (*Pandion haliaetus*) might teach their offspring to snatch fish from water, but the evidence is weak and anecdotal (Caro & Hauser, 1992). Meinertzhagen (1954) described how adults seemingly encourage their young to hunt by first refraining from feeding the fledglings (despite their begging) when adults had caught a fish, then repeatedly flying away with the fish in their talons, seemingly to encourage the young to follow. The fledglings were fed when they flew off the nest following the parents. On following days, adults would catch fish and drop it when they arrived in

proximity of the young. The adults would then catch the fish before it hit the water. The adults would repeat this behaviour until the young caught the fish after the adults had dropped it. This is suggestive of adults modifying their behaviour in the presence of naïve individual (first criterion). The offspring were then subsequently observed catching fish from the water (third criterion). Similar to the example of Florida scrub-jays, because this is an anecdotal report, there has not yet been an empirical evaluation of the potential cost of this behaviour (second criterion).

### 1.7.3 Invertebrates (honeybees)

Honeybees communicate the presence and location of nectar sources to their colony mates through waggle dances (von Frisch, 1965). Bees adjust the duration and rate of the waggle dance according to the profitability of the food source (first criterion) (Seeley, Mikheyev, & Pagano, 2000). In honeybees the waggle dance is a very effective process of recruitment of colony members to a specific food source (Riley, Greggers, Smith, Reynolds, & Menzel, 2005). Although most recruits take a straight path to the food source after witnessing a waggle dance (possibly the third criterion), not all bees reach the intended target without the use of other cues (Riley et al., 2005). This could be because learning is not perfect and only occurs a certain percentage of the time, and only with enough spatial resolution that it takes the bees to the rough area, after which they find the food using associated cues. However, it is not clear whether the primary function of the waggle dance is to elicit an immediate response or to promote learning, which would allow the recruits to direct themselves to the food source several times after the waggle dance. One can also question the value of learning in this case as food sources are easily depleted. Hence responding immediately to the dance signal would be beneficial but remembering the location of a food source for several days might not be beneficial if food is no longer available.

Trophallaxis is the exchange of liquid food by mouth, and is present in honeybees. Nectar in colonies is rapidly distributed among its members this way

(Gil & De Marco, 2005). It has also been found that bees acquire information through trophallaxis: they associate the scent of a solution with the reward (third criterion) (Gil & De Marco, 2005). The responses of the receiver are associated with long-term memory, as they remember the scent of the solution at least 46 hours after interaction (Gil & De Marco, 2006). The learned responses also increase with the concentration of sugar in the solution, but not with the duration of the trophallaxis interaction (Gil & De Marco, 2005). During trophallaxis donor bees are active, however it is not known if their primary motive is to feed another bee or transmit information, or whether donors preferentially transfer to naïve bees (first criterion). It has been found that after experiencing high reward, bees increase transferring food through trophallaxis (De Marco & Farina, 2001). However, bees also increased begging when resource uncertainty was higher (De Marco & Farina, 2003). Hence it is not known whether the donors or receivers are the main actor in the transfer. It would be interesting to know if bees use trophallaxis preferentially toward bees that do not "smell" of the same reward, which could be used as a proxy for knowledgeable or naïve individuals. Trophallaxis is also used during the waggle dance. Hence trophallaxis could transmit knowledge about the food source itself, on top of the waggle dance transferring information about its direction (Gil & De Marco, 2005).

Regarding the costs of these behaviour (second criterion), in the case of the waggle dance, dancers are at risk of increased competition for resources, and they also delay their next foraging bout, but there is no experimental evidence showing it is the case (Hoppitt et al., 2008). In the case of the trophallaxis interaction, to my knowledge, there has been no investigation of the cost of the transfers.

## 1.8 Taxonomic Distribution

Because teaching behaviour, and behaviour suggestive of teaching are so widely distributed in a variety of taxa, the distribution suggests that teaching has evolved independently. The presence of teaching in species not renowned for their cognitive abilities raises questions about previous assumptions that teaching requires "complex" cognitive abilities, at least when defined in functional terms (Pearson, 1989; Premack & Premack, 1996; Tomasello et al., 1993). In fact, the taxonomic distribution makes more sense if teaching is studied as an altruistic behaviour, rather than from a cognitive capacities perspective. Therefore, comparative studies of teaching in animals can help identify the ecological, but not the cognitive, underpinnings of this behaviour (Byrne & Rapaport, 2011). This is inevitable given the functional stance, which says nothing about underlying mechanisms. Furthermore, because it is not known how much intentionality plays a role in non-human teaching, comparing human to non-human teaching might identify the conditions under which teaching evolves, and thus shed light on the factors driving the evolution of human teaching, but it may not explain why the seemingly unique features of human teaching evolved, where many authors assume intentionality is key (Byrne & Rapaport, 2011). On the other hand, Thornton and McAuliffe (2012) argue that it is best to first find out whether a species teaches or not, before uncovering the cognitive mechanisms underpinning of this behaviour. Those mechanisms are likely to vary widely between species, and cases of teaching (Rapaport & Byrne, 2012) and some types of teaching would be considered uniquely human (Kline, 2015).

Evidence of teaching remains quite rare in the animal kingdom. However Thornton and Raihani (2010) think that it is not because it is not present in many species, but because it is difficult to collect the appropriate data that would satisfy all three of Caro and Hauser's (1992) criteria. Table 1.1 summarises the empirical evidence supporting teaching in the species mentioned in this chapter.

Table 1.1: Table summarising clear (experimental or statistical) evidence supporting the three criteria of Caro and Hauser's (1992) definition for all the species mentioned in 1.6, 1.7 and 1.9. A cross signifies insufficient evidence. [1] For the white-tailed ptarmigan, there is no evidence that the modified behaviour is costly to perform, but there is evidence that it does not benefit the hen

| Species | What is being taught? | First Criterion | Second Criterion | Third Criterion |
|---|---|---|---|---|
| Tandem-running ants | Location of food source | ✓ | ✓ | ✓ |
| Meerkats | Foraging manipulation | ✓ | ✓ | ✓ |
| Pied babblers | Response to vocalisation | ✓ | ✓ | ✓ |
| Superb fairy-wrens | Vocalisation | ✓ | ✓ | ✓ |
| Cheetahs | Hunting skill | ✓ | ✓ | × |
| Cats | Hunting skill | ✓ | × | ✓ |
| Tigers | Hunting skill | × | × | × |
| River otters | Hunting skill | × | × | × |
| Norway rats | Hunting skill | × | × | ✓ |
| African elephants | Oestrus | × | × | × |
| Killer whales | Hunting skill | × | × | × |
| Atlantic spotted dolphins | Hunting skill | ✓ | × | × |
| Chimpanzees | Tool use | × | × | × |
| Rhesus macaques | Locomotion | ✓ | × | × |
| Gorillas | Locomotion | × | × | × |
| Common big-eared bat | Foraging manipulation | ✓ | × | × |
| Florida scrub jays | Foraging extraction | × | × | × |
| White-tailed ptarmigans | Diet | ✓ | ×[1] | ✓ |
| Ospreys | Hunting skill | × | × | × |
| Honeybees | Location of food source | ✓ | × | *?* |
| Honeybees | Diet | × | × | ✓ |
| Golden lion tamarins | Diet | ✓ | × | × |
| Golden lion tamarins | Foraging substrate | ✓ | × | × |
| Domestic fowl | Diet | ✓ | × | × |

## 1.9 This Thesis

The aim of this thesis is to expand our understanding of the taxonomic distribution of teaching by investigating three suggestive cases, particularly focusing on the third criterion (social learning) of Caro and Hauser's (1992) definition, in three key suggestive cases. I examine putative instance of "fixed" teaching through (allo-) parental investment in hens (*Gallus gallus domesticus*) and golden lion tamarins (*Leontopithecus rosalia*), where adults may teach offspring what food is safe (golden lion tamarins) or unsafe (hens) to eat. I also examine a case where adults might teach their young what substrate is good to forage upon (golden lion tamarins).

### 1.9.1 Golden lion tamarins

#### 1.9.1.1 Food transfers

Golden lion tamarins in captivity were found to transfer more food that is novel to their young compared to familiar food (first criterion), potentially to teach them about their diet (Rapaport, 1999). It is not known however, whether adults incur a cost and whether the young learn from this behaviour. A more detailed account is given in Chapter 5 (5.2.4).

#### 1.9.1.2 Food-offering calls

Golden lion tamarins usually use food-offering calls to advertise that they are willing to transfer food to a juvenile. There are however reports in the wild of golden lion tamarin switching the context in which they use the call to attract juveniles to a foraging site (first criterion). It has been hypothesised that this is to teach the juvenile about the substrate properties in which prey can be found (Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002); however, similar to food transfers, there is no report as to whether this behaviour is costly or whether juveniles learn from it. A more detailed account is given in Chapter 6 (6.2.4).

### 1.9.2 Domestic fowl

Domestic fowl mothers have been found to change their behaviour when observing their chicks feed from seemingly unpalatable food compared to palatable food (first criterion) (Nicol & Pope, 1996). Similar to evidence in golden lion tamarins, it is not known whether this change of behaviour comes at a cost to the hen and whether the chicks learn to switch from the seemingly unpalatable to the palatable food source. A more detailed account is given in Chapter 7 (7.2.2).

### 1.9.3 Overview of this thesis

In the two following chapters, I will give an overview of the ecology and behaviour of golden lion tamarins (Chapter 2) and domestic fowl (Chapter 3), with an emphasis on their social behaviour in relation to teaching. In Chapter 4, I will introduce the different statistical approaches used in this thesis, and provide a description of the philosophy underlying these approaches.

In Chapter 5, I examine the case of food transfers in wild golden lion tamarins as suggestive evidence for teaching. In that chapter, I first look at the tutors' behaviour when juveniles are young, to determine whether adults transfer more novel food compared to familiar food to their young. I then use Bayesian models to explore whether previous experience affects juveniles' future food choices, with a particular emphasis on food transfers. This allows me to assess the first and third criteria of Caro and Hauser's (1992) definition in the putative case of teaching in golden lion tamarins through food transfers.

In Chapter 6, I turn to the case of food-offering calls in wild golden lion tamarins. I use playbacks to assess whether juveniles learn that a particular novel substrate constitutes a good foraging substrate from exposure to food-offering calls. Comparisons were made between groups that had access to the novel substrate with a normal rate of food-offering calls, and groups that had access to the novel substrate with increased rate of food-offering calls through

playbacks, to establish whether there were any foraging differences due to food-offering calls. This allows me to assess the third criterion of Caro and Hauser's (1992) definition in the putative case of teaching in golden lion tamarins through food-offering calls.

In Chapter 7, I expand on previous findings to analyse whether domestic fowl chicks learn what food to feed from, based on the hen's demonstration. This was done by training hens to feed from one of two coloured foods by making one coloured food unpalatable. Chicks were then exposed to demonstrator hens, and the chicks' foraging choices were then assessed on four days following the demonstration. This work builds on Nicol and Pope's (1996) findings that hen modify their behaviour based on chicks seemingly making foraging errors. This allows me to assess the third criteria of Caro and Hauser's (1992) definition in the putative case of teaching in domestic fowl through the maternal foraging display.

In Chapter 8, I discuss my findings in the context of the previous literature on teaching in animals and suggest directions for future work.

# Chapter 2:

# The phylogeny, ecology and behaviour of wild golden lion tamarins

## 2.1 Abstract

In this chapter, I will give a short introduction to golden lion tamarins (*Leontopithecus rosalia,* Linnaeus 1766) (henceforth GLTs), and their phylogenetic relationships to other primates, particularly within the Callitrichidae family. I will discuss what differentiates this family, as well as the *Leontopithecus* genus, from other primates. I will then describe their habitat, particularly the localities used in the experiments in Chapters 5 and 6. I will then explain behaviour patterns in this species that are particularly relevant to the experiments reported in this thesis, specifically, communication, foraging and social behaviour. Finally, I will give details about the field sites and subjects used in this thesis.

## 2.2 Taxonomy

Golden lion tamarins are a small, diurnal species of arboreal new world primate (Dietz, Baker, & Miglioretti, 1994) that belong to the Callitrichidae family. Callitrichidae is a family of new world monkeys that also includes 42 species split into seven genera: *Saguinus* (tamarins – 15 species), *Leontopithecus* (lion tamarins – four species), *Callimico* (Goeldi's monkey – one species), *Callithrix* (eastern Brazilian marmosets – six species), *Callibella* (Roosmalens' dwarf marmoset – one species), *Cebuella* (pigmy marmoset – one species) and *Mico* (Amazonian marmosets – 14 species) (Cortes-Ortiz, 2009). Callitrichidae are the smallest anthropoid primates (weighting 110-750 grams), and most species, including GLTs are not sexually dimorphic (K. Brown & Mack, 1978). However, Hershkowitz (1977) reports some structural difference in the laryngeal sac of males (enlarged) and females (reduced or absent), which might influence acoustic features.

Within the Callitrichidae family, GLTs belong to the *Leontopithecus* genera (lion tamarins). Lion tamarins are the largest species belonging to this family, and all are endemic to the Atlantic forest, on the south-eastern coast of Brazil. Over the years, lion tamarins have been classified as different subspecies

(Hershkowitz, 1977) or species (Groves, 1993), but they are now considered as four distinct species. Species identification has been made through coat coloration, ecological-adaptive difference and craniodental measurements (Rosenberger & Coimbra-Filho, 1984). The three other species are: *L. chrysomelas* [golden-headed lion tamarin (henceforth GHLT), Kuhl 1820], *L. chrysopygus* [black lion tamarin (henceforth BLT), Mikan 1823], and *L. caissara* [black-faced lion tamarin (henceforth BFLT), Lorini & Persson 1990]. Figure 2.1 shows the remaining distribution of the four lion tamarin species.

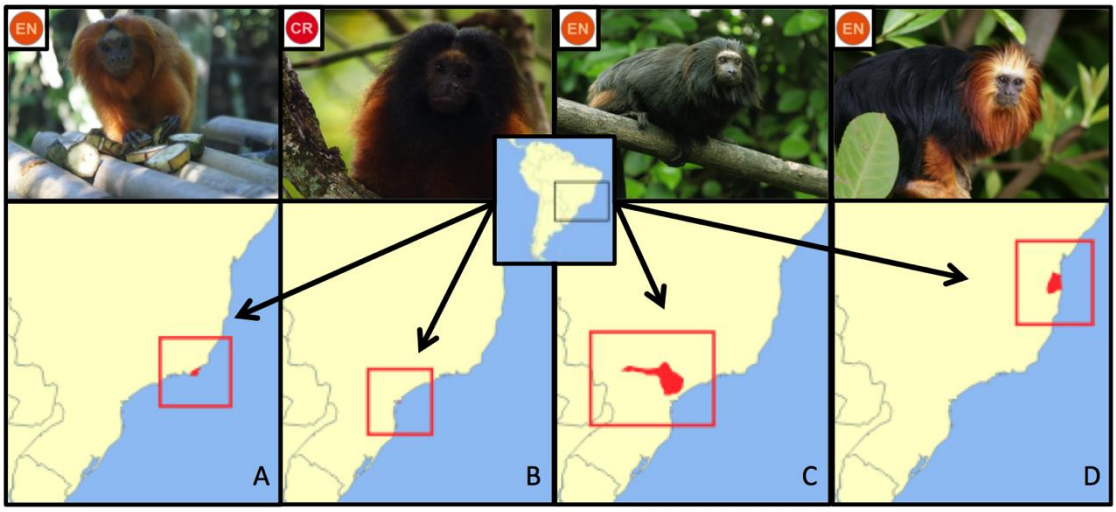


Figure 2.1: Lion tamarins (Leontopithecus spp.), their distribution and status according to the IUCN Red List. (A) Golden lion tamarin (*L. rosalia*), native to the Atlantic Forest in the state of Rio de Janeiro, Brazil. Endangered. (B) Black-faced lion tamarin (*L. caissara*), native to the states of Paraná and São Paulo, Brazil. Critically Endangered. (C) Black lion tamarin (*L. chrysopygus*), native to the state of São Paulo, Brazil. Endangered. (D) Golden-headed lion tamarin (*L. chrysomelas*), native to the state of Bahia, Brazil. Endangered

## 2.3 Life history and morphology

There is one main feature that sets Callitrichidae apart from other primates, both in terms of physiology and behaviour: their reproductive strategy. GLTs, like most species of callitrichids, are mainly monogamous. One study reports a high incidence of polyandrous group structure (approximately 40% of groups contrained two non-natal adult males), but the dominant male was usually able to monopolise the female around the time of conception (Baker, Dietz, & Kleiman, 1993). Another study also found evidence of polygyny in approximately 10% of the groups studied (Dietz & Baker, 1993). Callitrichidae also have a

particular reproduction strategy: they are cooperative breeders that have an extremely rapid reproductive turnover. In fact, despite their small size, three of the most distinguishable features of this family are giving birth to multiple young (usually twins), rapid maturation and intense parental investment. In GLTs, about 78% of parturitions are twins (Dietz et al., 1994). Parental care for twins would require an incredible amount of energy, and is usually quite rare in other primate species. The overall high reproductive turnover strategy that GLTs seem to have adopted is probably evolutionarily linked to their cooperative breeding system. Twins are the norm in most Callitrichidae species that have been studied, and there can be two to three litters a year (K. Brown & Mack, 1978). In anthropoid primates, much of the necessary behaviour for survival and reproduction is learned during a lengthy maturation period. Callitrichidae lack this lengthy maturation period, and therefore might encounter difficulties learning the necessary behaviour for survival. Teaching behaviour might therefore have evolved to reduce the length of learning.

Another feature that distinguishes Callitrichidae from other primates is their claw-like nails (tegulae) that allow them to cling vertically to tree trunks while exploiting food resources (Garber, 1992; Sussman, 2000). Most primates have flat nails (ungulae). However, unlike other Callitrichidae, lion tamarins have specialised narrow, elongated hands and fingers to use in extractive foraging. In *Leontopithecus* species this adaptation has allowed individuals to develop specific manipulative foraging skills, which enables them to probe for concealed protein-rich prey from small knotholes, bromeliads, tree crevices, and similar substrates, as well as to allow them to strip bark off trees to locate concealed insects and small vertebrates (Dietz, Peres, & Pinder, 1997; Garber, 1992). Those elongated fingers allow *Leontopithecus* species to obtain prey from substrates that are not available to other callitrichid species (Rylands, 1989). This kind of prey extraction is considered quite complex because of the sensorimotor coordination and learning required (Gunst, Boinski, & Fragaszy, 2010). Lion tamarins depend on more manipulation and explorative foraging to survive, compared to other genera such as *Saguinus* (tamarins) and *Callithrix* (marmosets), which primarily rely on visual foraging to obtain prey on the

surface (Garber, 1993). In captivity, lion tamarins have also been found to be less neophobic and more innovative than those other species, and research suggests that it is because of their foraging requirements in the wild (Day, Coe, Kendal, & Laland, 2003).

## 2.4 Habitat

GLTs inhabit both primary and secondary Atlantic rainforest (Ferraz, 2013); this terrain is one of the five most important biological hotspots, with 32% of mammal species being endemic, but is also one of the most threatened ecosystems in the world with only less than 8% of the original cover still remaining (da Fonseca, 1985; da Fonseca, Herrman, & Leite, 1999; INPE, 2002; Myers, Mittermeier, da Fonseca, & Kent, 2000). The GLTs' habitat is now restricted to the Sao Joao River Watershed (Coimbra-Filho, 1969; Dietz et al., 1997; Rylands, 1993).

One of the main places to find GLTs is at the Poço das Antas Biological Reserve, created in 1974. The Poço das Antas Biological Reserve (22 °30'-22 °33' S; 42 °15'–42 °19' W) is located in the Silva Jardim county of the Rio de Janeiro State, Brazil. It contains various types of forests, such as secondary growth and climax forest, hillside and swamp forest (Dietz et al., 1997) (see Fig. 2.2). Around the protected area are pockets of remnants of the Atlantic forest in which some groups of GLTs can be found. Fragmentation of the forest is mainly due to farming practises.

GLT groups travel, forage, and sleep together (Dietz et al., 1997). They sleep in tree holes, preferentially those that are between 11 and 15 m off the ground, and can travel up to 1.5 km a day to find food sources (Dietz et al., 1997; Hankerson, Franklin, & Dietz, 2007). Lion tamarins are one of the few primate species that repeatedly use the same tree holes for the majority of their sleeping sites (Hankerson et al., 2007). Sleeping holes are thought to have several functions, ranging from protection from weather, predators, parasites, disease, and provisioning of proximate early morning and late afternoon access to

foraging sources (see Hankerson et al., 2007). Predators include raptors, felids, snakes and other small arboreal carnivores (Kierulff et al., 2002).

Figure 2.2: Brown howler monkey (*Alouatta guariba*) at the Poço das Antas Biological Reserve, where the forest is particularly dense

## 2.5 Behaviour

I will now discuss specific behaviours of the species that are of relevance to the experiments I conducted. Both experiments look at social learning in a foraging context, with the experiment in Chapter 5 examining the role of food transfers in juveniles' foraging decision, and the experiment in Chapter 6 investigating the role of food-offering calls in juveniles' foraging decision. The behaviour I will now describe are vocal communication, foraging behaviour and a broader section on social behaviour, particularly focusing on juveniles and their interactions with other group members.

### 2.5.1 Vocal communication

GLTs are an arboreal species, living in dense tropical forests, and use acoustic signals as the main mode of communication. Different call types are used in specific contexts and correlate with specific behaviour patterns (Ruiz-Miranda & Kleiman, 2002). Ruiz-Miranda and Kleiman (2002) have made a full list of calls, their description and context. For instance, "clucks" are predominantly heard

during foraging bouts (Boinski, Moraes, Kleiman, Dietz, & Baker, 1994), "whine" calls as an alarm, and multisyllabic "long-calls" for group cohesion and intergroup spacing (Boinski et al., 1994; Ruiz-Miranda & Kleiman, 2002). Vocal communication is particularly important as GLTs travel great distances and have territories to defend. GLTs can also combine different call types. For example, "trill-raps" are used by begging young to seek attention, protection or food, "trill-whines" to startle predators or withdraw, and "cluck-whines" as aggression or defence (see Ruiz-Miranda & Kleiman, 2002, for full description). Lion tamarins have also been found to have different vocalisations for aerial versus terrestrial predators (M. I. Castro, Beck, Kleiman, Ruiz-Miranda, & Rosenberger, 1998) and the rate of food calls varies with food preference (Benz, 1993).

It is interesting to note that the food-offering calls of GLTs are really different, both in form and function, from any vocalisation reported in other Callitrichidae species. Food-offering calls in GLTs most resemble their food calls; however, food-offering calls are rarely used to beg for food. Rather, they are used as a signal to juveniles to take food from calling adults (K. Brown & Mack, 1978). The food-offering call is also potentially used for teaching juveniles what substrates are good to forage on, which is of relevance for the experiment in Chapter 6 (Rapaport, 2011). A spectrogram of a food-offering call is provided in Figure 2.3.

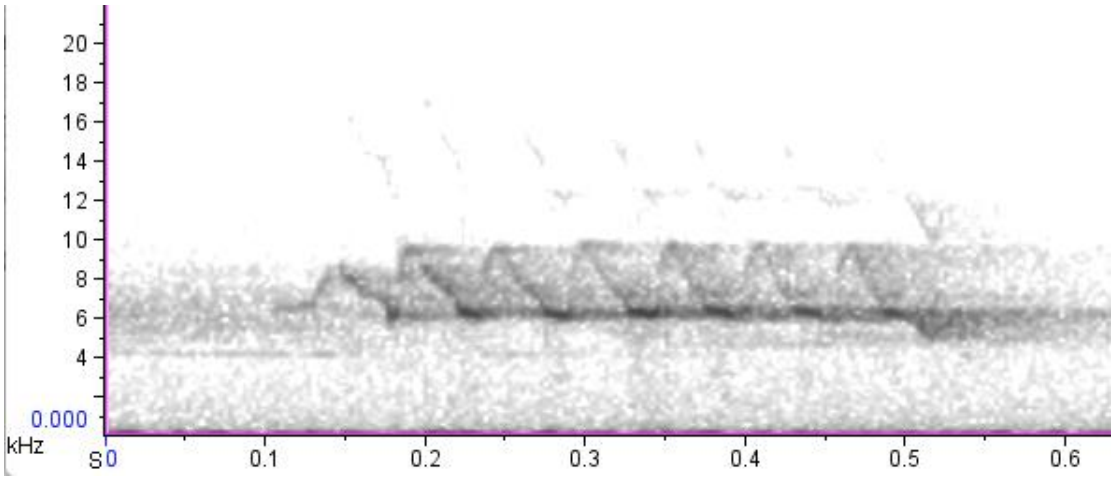


Figure 2.3: Spectrogram of one of the food-offering calls used in the experiment presented in Chapter 6.

There have been some age and sex differences observed in vocalisation production. For instance, males emit more "trills" and nontonal vocalisations

than females (McLanahan & Green, 1978), while immature GLTs vocalise up to three times more than adults (Ruiz-Miranda, unpublished data).

### 2.5.2 Foraging ecology

#### 2.5.2.1 Diet

GLTs are opportunistic omnivores, and have a very varied diet which ranges from fruits, nectar, insects, other invertebrates, small vertebrates, exudates, bird eggs and fungi (Dietz et al., 1997; Lapenta, Procópio-De-Oliveira, Kierulff, & Motta-Junior, 2003; Rylands, 1989). They also ingest seeds of between 68-78% of the fruiting plants that they eat, and therefore play an important role in forest regeneration by disseminating those seeds (Lapenta et al., 2003; Lapenta, Procópio-de-oliveira, Lapenta, & Procópio-de-oliveira, 2008). GLTs however feed mainly from fruits and animal prey (Peres, 1989a), and their diet varies constantly due to the seasons and sometimes due to between-group migration (Dietz et al., 1997; Kierulff et al., 2002). In a study looking exclusively at females (n=10), Miller et al. (2006) found that the diet of GLTs varied from consisting of 82% of plant and 18% of prey during the dry season, which corresponded to the non-reproductive period, to a diet consisting of 68% of plant and 32% of animal prey during the wet season, which was also the season during which females were pregnant or lactating. Overall, Miller and Dietz (2005) found that GLTs tend to consume more food during the dry season compared to the wet season. Another study looking at GLTs of both sexes also found considerable seasonal variation (Dietz et al., 1997). When ripe fruits were available, the diet of one of the studied groups consisted of 78.4% of ripe fruits, 13.6% of animal prey, 5.6% of unripe fruit, 1.5% of exudates and 0.9% of palm nuts. For the same group, the next year had low fruit availability, and ripe fruits only consisted of 31.8% of the diet, while floral nectar was eaten the most, and consisted of 43.4% of the diet, followed by 16.1% of animal prey, 6.5% of unripe fruits, 1.3% of exudates, and GLTs were also observed eating flowers 0.4% of the time (Dietz et al., 1997). This shows how flexible GLTs are when it comes to their diet, and the impact that seasonal variability has on the GLTs diet.

In this same study, two groups of GLTs were reported feeding from 40 plant species, with 13 of those species making 80% of their diet, while another group was observed feeding from 45 plant species, with only eight species accounting for 80% of their diet (Dietz et al., 1997). Overall, Dietz et al. (1997) found 64 plant species that GLTs fed on, spanning across 23 families. In another study, 24 species of plant accounted for 70% of the time spent feeding on plant material, and 54 plant species accounted for 94% of that time, showing that GLTs rely on a variety of species (see Table 2.1 for the list of species) (Miller & Dietz, 2005). Of this time spent feeding on plants, 88.3% was spent eating fruits, 10.4% was spent feeding on nectar from *Symphonia globulifera* flowers, and 1.3 % was spent feeding on exudates. Feeding on exudates are indeed rare feeding events, and in another study only accounted for 1.5% of all feeding events (Peres, 1989b). This was only observed during the dry season in Peres (1989b), when fruit availability was particularly low. In fact, although, the bulk of GLTs' diet consists of fruits, this resource is particularly susceptible to seasonal fluctuations. GLTs therefore have to switch to other sources, such as nectar or exudates, for carbohydrates (Dietz et al., 1997; Garber, 1984; Peres, 1989b). GLTs do not feed from exudates all year long, because unlike *Callithrix sp* they do not have a larger and complex caecum which helps digesting the complex carbohydrates contained in gums (Coimbra-Filho, Da Cruz Rocha, & Pissinatti, 1980; Power & Oftedal, 1996). Exudates come mainly from two genera of plants: *Macherium sp* and *Parkia sp* (Peres, 1989b), and are usually collected opportunistically: in one study, GLTs were observed feeding on exudates only when tree gouges had previously been made by marmosets (*Callithrix sp*) (Ruiz-Miranda et al., 2006). However, in another study, there were reports of GLTs actively biting into the base of *Machaerium* lianas to obtain exudates (Peres, 1989b). Juveniles were however seen to be unable to do so, and only obtained exudates from lianas that were no longer occupied (Peres, 1989b).

Table 2.1: Table listing percent of time spent feeding on fruits, nectar and exudates corresponding to the plant species that could be identified, from Miller and Dietz (2005).

| Scientific name or common name | Percent time feeding | Caloric value (kcal/g dry matter) |
|---|---|---|
| *Cecropia hololeuca* | 11 | 5.097[a] S |
| *Symphonia globulifera* (nectar) | 11 | — |
| *Miconia* sp. 2 | 9 | 4.881[a] S |
| *Miconia cinnamomifolia* | 7 | 4.871[a] S |
| *Henriettea saldanhei* | 6 | 4.013[a] S |
| *Miconia prasina* | 6 | 3.986[a] S |
| *Euterpe edulis* | 5 | 3.987 |
| *Ficus clusiifolia or obtusiuscula* | 5 | 4.966[a] S |
| *Eugenia moraviana* | 4 | 4.028 |
| *Myrcia racemosa* | 4 | 5.372 |
| Unknown fruit sp. 1 | 4 | 4.165 |
| *Cordia sellowiana* or *taguayensis* | 3 | 3.842 |
| *Musa* sp. 1 | 3 | 3.986 |
| *Myrtaceae* sp. 3 | 3 | 4.068 |
| *Symphonia globulifera* (fruit) | 2 | 4.375 |
| *Anacardium occidentale* (exudate), *Mimosa bimucronata* (exudate) | 1 | 4.127 |
| *Eugenia cf. capparidifolia* | 1 | 4.052[a] SK |
| *Monstera* sp.1 | 1 | 3.707 |
| *Genipa americana* | 1 | 3.963 |
| *Lacistema pubescens* | 1 | — |
| *Plinia* sp. 1 | 1 | 3.940 |
| *Myrcia anceps* | 0.9 | 4.947 |
| *Bactris setosa* | 0.8 | 3.877 |
| *Psidium guaiava* | 0.7 | 3.683 |
| *Unknown fruit* sp. 3 | 0.7 | — |
| *Miconia albicans* | 0.6 | 4.270[a] S |
| *Miconia* sp. 1 | 0.6 | 4.285[a] S |
| *Asplundia brachypu* or *Thoracocarpus bissectus* | 0.5 | 5.839[a] S |
| *Ficus* sp. 1 | 0.4 | 4.728[a] S |
| *Inga thibaudiana, affinis, cordistipula or letpantha* | 0.4, 0.4 | 4.410, 4.274 |
| *Miconia staminea* | 0.4 | 4.292[a] S |
| *Tournefortia breviflora* | 0.4 | — |
| *Tovomitopsis paniculata* | 0.4 | 4.129 |
| Unknown fruit sp. 2 | 0.4 | 4.633 |
| Unknown fruit sp. 4 | 0.4 | 4.335 |
| *Cecropia glaziovii or lyratiloba* | 0.3 | 4.535[a] S |
| *Elaeis guineensis* | 0.3 | 7.333 |
| Urticaceae sp. 1 | 0.3 | — |
| *Syzygium jambos* (fruit) | 0.3 | 3.926 |
| Myrtaceae sp. 5 | 0.2 | 4.023 |
| Unknown bromeliad sp. 1 | 0.2 | 3.720 |
| *Monstera* sp. 2 | 0.1 | 3.714 |
| *Faramea multiflora* var. *salicifolia* | 0.1 | 3.913 |
| *Hirtela* sp. 1 | 0.1 | — |
| *Marlierea* cf. *glazioviana* | 0.1 | — |
| Myrtaceae sp. 1 | 0.1 | — |
| Myrtaceae sp. 2 | 0.1 | 4.433 |
| Myrtaceae sp. 4 | 0.1 | 4.244 |
| *Pradosia latescens* | 0.1 | 4.572 |
| *Tapirira guianensis* | 0.1 | — |
| Unknown fruit sp. 5 | 0.1 | 4.775[a] S |

Regarding their consumption of fruits, GLTs prefer fruits that are usually small, pulpy, sweet and soft (Coimbra-Filho & Mittermeier, 1973; Dietz et al., 1997). By studying the properties of the fruits eaten by GLTs, Lapenta et al. (2003) found that the mean fruit length and width were 18.6 ±11.1 mm and 15.6 ±8.4 mm. Larger fruits are only consumed occasionally (Dietz et al., 1997). In one study, the most common fruits eaten came from two genera of Melastomacoeae: *Clidemias* and *Miconia* (Dietz et al., 1997). *Miconia* plants are mainly found on hilltops and newly planted corridor forests, while *Climedia* plants are mainly found in more humid soils at lower elevation (Dietz et al., 1997). The species present in GLTs' diet are therefore highly dependent on the habitat type found in their territory. Moreover, although GLTs eat a wide variety of fruits, those are very patchily distributed, and are ephemeral nutritional resources (Dietz et al., 1997). The time spent consuming the fruit of a particular plant species was found to be significantly positively correlated with the energy content per gram of dry fruit matter (Miller & Dietz, 2005).

In a study by Miller and Dietz (2005), from the 128 observations made of GLTs eating animal prey, 75% of those prey were orthopteran, 10% were roaches, 7% were frogs, 4% were larvae, 2% spiders, 1% lizards and 1% walking sticks. Dietz et al. (1997) also reported GLTs feeding on snakes, and occasionally on snails and nestling birds, and found out that insect larvae that were eaten by GLTs were Coleoptera and Lepidoptera larvae. They also give two examples of species of frogs that GLTs were observed feeding on: *Hyla bethalutzae* and *Dendrophryniscus brevipollicatus* (Dietz et al., 1997). Although millipedes, centipedes and aposematic hemipterans were really abundant in GLTs' environment, they were rarely eaten by them (Dietz et al., 1997), suggesting that GLTs have specific feeding preferences or that some prey are not palatable to them. In fact, Dietz et al. (1997) occasionally observed GLTs vomiting or salivating extensively after ingesting a prey, further supporting the fact that some items are unpalatable or noxious to GLTs. The majority of animal prey are non-mobile concealed prey found in palm crowns, bromeliad axils, wooden crevices such as knotholes and crevices, and under bark (Dietz et al., 1997; Garber, 1992; Kleiman et al., 1986; Peres, 1989a), and captures of mobile prey on

foliage or flying were rare: only 2% of 318 observed prey captures (Dietz et al., 1997). Compared to exposed prey, embedded prey vary less across seasons (Peres, 1989a). Those concealed environments provide stable microhabitats for small invertebrates, particularly during the dry season, but those microhabitats are also easily depletable (Peres, 1989a). 98% of prey captures came from those small, discrete microhabitats (Peres, 1989a). GLTs therefore have to learn what type of habitats are likely to host prey, but cannot rely on a specific location to find those prey.

GLTs are solitary hunters when they forage for animal prey, however, there might be several GLTs feeding on fruit in the same fruit tree. Hence unsurprisingly, Miller and Dietz (2005) found that group characteristics, such as group size, were more likely to explain variation of time spent feeding on plant matter, while individual characteristics, such as age, were more likely to influence searching for animal prey. However, there is overall little individual variation in the time spent consuming prey, suggesting that there is a uniform protein requirement among GLTs (Miller & Dietz, 2005). Although prey constitute less than 25% of GLTs' diet, they provide important nutrients, as suggested by Stoinski and Beck's (2004) study that found that during reintroduction of GLTs, the time spent micromanipulating prey during the first six month of reintroduction, was correlated with individual survival.

GLTs are active 9-12 hours a day, according to the photoperiod, but mainly forage on plants between 07:00 and 08:00, and on prey items between 09:00 and 13:00 (see Kierulff et al., 2002). This pattern could potentially be explained by the fact plants contain more water earlier in the morning because of the dew, and prey items might be more active later in the morning as the day warms up.

#### 2.5.2.2 Foraging tasks in captivity

In captivity, experimental work with novel tasks showed that although neophobia was the same across age class, adults were the first to manipulate the

task successfully (innovate), compared to younger individuals (Day et al., 2003). This could be due to their increased sensory-motor development.

For GLTs, both fruits and animal prey are locally abundant but are patchily distributed (Dietz et al., 1997). This distribution of resources could have led to the large home ranges that GLTs have compared to other callitrichid species (Dietz et al., 1997). GLTs therefore have to travel a lot in order to feed on those food patches (Dietz & Baker, 1993; Peres, 1989a; Platt, Brannon, Briese, & French, 1996). Because of their big home ranges and the spatial distribution of the resources, GLTs are thought to be good at spatial memory and navigation (Platt et al., 1996). When comparing the performance of Wield's marmoset (*Callithrix kuhlii*) to GLTs on a spatial memory task, Platt et al. (1996) found that the marmosets initially outperform GLTs on short-term memory tasks, but that when required to memorise the location of food over 24h or 48h GLTs outperform marmosets. They suggest that this is linked to their foraging strategy: Wield's marmoset forage on less depletable food sources compared to GLTs, and usually revisit food sources within 24h. However, it can take several days or weeks for GLTs to revisit a foraging site, due to the size of their range. A slow decay in memory would allow GLTs to be more likely to find food in widely separated foraging sites and hence increase their foraging efficiency (Platt et al., 1996).

Despite the short maturation period of GLTs, there are a multitude of skills juveniles need to acquire in order to become successful adults. Not only is their social environment complex, but so is their physical environment, with patchy resources constantly changing in their distribution. The GLTs' diverse diet might require a large degree of exploration and learning to fully master. Hence, due to the complexity of their diet, social learning might be particularly beneficial for the young to acquire important information and foraging skills. Social learning could play an important role in increasing their survival or decreasing their latency to independence (Rapaport & Brown, 2008). However, the role of social learning and teaching in the adoption of food preference or diet has never been directly tested in GLTs.

#### 2.5.2.3 Food transfers

Unlike most primates, GLTs actively provision young and other group members with solid foods (Rapaport & Brown, 2008). Food transfers occur in at least 10 species of Callitrichidae and in at least five species , including in GLTs, there is evidence of adults vocalising to infants to offer food (Feistner & Price, 1991). Experimental studies show that GLTs preferentially transfer food items that are rare, difficult to process or novel to juveniles (Feistner & Chamove, 1986; Moura, Nunes, Langguth, & A. Moura, 2010; E. C. Price & Feistner, 1993; Rapaport, 1999, 2006) but adults also transfer food to pregnant females (Ruiz-Miranda et al., 1999). The energy invested in order to obtain a food item from a foraging task influences food transfer behaviour towards other adults, highlighting the costly nature of this behaviour (Rapaport, 1998). The transferring of novel foods from adults to juveniles is thought to be a candidate case for teaching behaviour as juveniles might be able to learn a wider breadth of diet through this behaviour. More details of food transfers from adult to young will be discussed in the next section, Social Behaviour (2.5.3).

### 2.5.3 Social behaviour

GLT groups usually consist of 2 to 11 individuals and are mainly kin based (mean group size of 5.4; the mean group size of the groups used in the experiments was 7.2) (Dietz & Baker, 1993; Dietz et al., 1994). Each group includes a single breeding female, one or more potentially breeding males, and offspring born within the group (Baker, Bales, & Dietz, 2002). Most GLTs disperse from their natal groups, mainly immigrating to neighbouring groups, with 60% of individuals disappearing from their natal group by three years of age and 90% after four years (see Baker et al., 2002).

GLTs defend a territory of approximately 45.2 ± 15.5 ha against other GLT groups (Dietz et al., 1997). During territorial encounters, there is more locomotion and vocalisation than during non-encounter contexts, and they also react to the presence of other groups on the basis of vocal cues (Peres, 1989a).

However, within groups, there is a high degree of tolerance and cohesiveness, which might promote social learning (Coussi-Korbel & Fragaszy, 1995). Moreover, there are no reports of infanticide in *Leontopithecus*, supporting the notion that the genus shows high social tolerance (see Santos, French, & Otta, 1997). However, there are reports of such behaviour in free-ranging common marmosets (*Callithrix jacchus*), a closely related species (Digby, 1995).

#### 2.5.3.1 Cooperative breeding and juvenile development

GLTs are cooperative breeders, where most juveniles remain in the group as adults and provide help in raising subsequent litters. Alloparental care is thought to have evolved to reduce the energetic demands of parental care (Goldizen, 1990). In GLTs, there are huge costs of reproduction, especially for the breeding females, as they usually have twin infants, with a high infant to adult ratio weight (twins can weigh up to 25% of the mother's weight), and a pregnancy that can overlap with lactation (several litters a year) (French, 1983; Tardif, 1994). Although all members of the groups participate in the care of the young, Tardif et al. (2002) found that in lion tamarins, breeding females contribute more to infant care than in other Callitrichidae species, and the infant care is quite intense with lactation, carrying of infants and provisioning of solid food (Tardif, 1994). However, all subadults and adults take care of the young, and provide alloparental care through carrying infants that are not their own, provisioning them with food and defending them against predators (Garber, Moya, & Malaga, 1984; Terborgh & Goldizen, 1985). Moreover, helpers also play an active role in provisioning parents that have newborn offspring (K. Brown & Mack, 1978). However, Siani (2009) found that despite the help provided, parents contribute significantly more to infant carrying and food provisioning than helpers.

##### *2.5.3.1.1 Carrying*

GLTs take longer to mature, compared to other Callitrichidae species, potentially because of their slightly bigger size, and infants require more help from non-breeders to increase their chances of survival. For instance, carrying of

infant GLTs occurs from birth to approximately 12/14 weeks of age (Hoage, 1982; Ruiz-Miranda et al., 1999), whereas, in other Callitrichidae species infants become independent of carriers much earlier [by 8 weeks for *Callithrix jacchus* (Tardif, Carson, & Gangaware, 1986; Tardif, Harrison, & Simek, 1993)].

Mothers are the main carriers of infants in the first three weeks (Hoage, 1982). However, unlike most primate species, male Callitrichidae of some species (BLTs) can invest as much in parental care as females, and become the predominant carriers after the first three weeks (Tardif et al., 2002). It was also found that older helpers (adults) carry more than younger ones (juveniles and subadults) (Santos et al., 1997). This could be due to the physiological constraint of the help provided.

*2.5.3.1.2 Food transfers*

After carrying, infant care continues in the form of solid food provisioning from weeks 4-36 (Ruiz-Miranda et al., 1999). Most non-Callitrichidae primates do not actively provision offspring, and the high rate of seemingly voluntary food transfers and signalling prior to food transfers seems unique to Callitrichidae (K. Brown & Mack, 1978; Rapaport & Ruiz-Miranda, 2006). Food transfers are indeed an important aspect of alloparental care in GLTs. Physical maturation is rapid in GLTs, completing at 2-4 months of age (Hoage, 1982) and reproductive maturity can be as early as 17 months (French & Inglett, 1989). However, because of their complex foraging diet, food transfers by all group members should increase the growth rate of juveniles even after weaning, by allowing them easier access to food items (Garber & Leigh, 1997). Furthermore, food transfers may also allow juveniles to learn about the diet (Rapaport, 1999) by allowing them to forage independently earlier before the birth of the next litter, and might qualify as a case of teaching. However, learning through food transfers has never been directly shown.

In a study on infants <12 weeks old, Siani (2009) found that 174/199 of food transfers between caregivers and infants were successful. But as juveniles

get older and their success at foraging independently increases, the rate of food transfers drops (Rapaport, 2011). The shift to foraging independently usually takes place between the 21-33 week-old period and the 33-44 week-old period, and it is also during this period that the decrease of food transfers is observed.

#### 2.5.3.2 Costs and benefits to helpers

Provisioning by helpers could directly increase offspring survival by giving juveniles benefits from foraging activity of all members and decrease the cost of having offspring for the breeders. The cost of rearing offspring in GLTs is high, moreover, the omnivorous foraging diet is diverse and juveniles might require a long time to acquire the appropriate knowledge of edible food items (Bales, Dietz, Baker, Miller, & Tardif, 2000; Garber & Leigh, 1997). Distributing the burden of infant care amongst multiple individuals is therefore a solution to reduce the short-term energetic demands of infant carrying for the breeders. Carriers were also found to mediate the cost of infant care through behavioural changes rather than physiological ones, with helpers showing no weight loss in one study (Siani, 2009). However, in previous studies, carrying infants in Callitrichidae species has been linked to weight loss (Sánchez, Peláez, Morcillo, & Gil-Bürmann, 2005), increase of caloric cost of travel (Tardif, 1997), and reduced foraging behaviour (Goldizen, 1987; E. C. Price, 1992). Moreover, it was suggested that the presence of helpers might directly affect the survival of the offspring, particularly because of their important role in offspring provisioning. For instance, in the wild, it was found that the number of male helpers was correlated with the number of surviving infants, but not the initial number of infants. This increased survival may be due to behaviours other than direct infant care, such as territorial defence (Bales et al., 2000). However, in another study that included several *Leontopithecus* species, it was found that group size did not directly affect infant independence (Santos et al., 1997). Moreover, in the first three months of age, group size, and therefore the number of helpers, had little effect on the amount of maternal carrying effort in lion tamarins, whereas fathers carried their infants less if there were more helpers around (Santos et al., 1997). This suggests that if helpers do alleviate some of the cost of parental care,

such as energetic cost of lactation, it is independent of the maternal carrying effort. This is supported by the finding that in free-ranging groups of GLTs, the number of helpers assisting with infant carrying does predict the reproductive tenure of males but not females. Reproductive males might benefit more from the number of helpers than reproductive females because their investment in infant care declined as the number of helpers increased (Bales et al., 2000).

In some Callitrichidae groups, although group structure is usually based on kin, there are some non-related individuals that stay in the groups and participate in infant care. Huck et al. (2004) suggest that in moustached tamarins (*Saguinus mystax*), the presence of non-related individuals may happen because non-related individuals could either increase their chance of inheriting the main breeding position, or increase their chance of mating because of the polyandrous mating by the female.

Overall, data in GLTs seem to support the hypothesis that energetic costs have driven the evolution of cooperative care in this species (Siani, 2009), and that cooperative breeding systems in Callitrichidae promote transfer of information about food transfer of food between caretakers and offspring (Snowdon, 2001). Due to the rapid turnover and birth of twins, mothers would not be able to care for their young on their own, and therefore require the help of group members. Although those alloparents forego reproduction for that period, they still increase their inclusive fitness by helping increase the survival of relatives (Bales et al., 2000). It has also been shown that helpers gain relevant parental experience, with French et al. (1996) finding that the offspring of females with previous helping experience had higher chances of survival, than ones who had mothers that had never carried or cared for an infant previously.

## 2.6 This study

Given their endangered status on the IUCN Red List, most studies of wild GLTs concentrate on the species' interaction with their environment. However, given their group living structure, cooperative breeding, and high rates of social

behaviour, they are an ideal species in which to study social learning, particularly between adults and young. There are currently no studies looking at social learning in wild GLTs, and the ones closest to this topic were made on captive individuals. Studying social learning could also have a major impact on the preservation of the species, because of the potential for cultural transmission. Stable traditions can re-structure populations based on distinctive cultural variants. This structure might have allowed sub-populations to adapt to their environment in different ways. Whitehead et al. (2004) highlight that culture can be an important determinant of behaviour in some species, and this could have repercussions for population biology and conservation. The reduction of population size could lead to a removal of cultural diversity without necessarily compromising genetic diversity (Laiolo & Jovani, 2007). There is therefore increased attention towards "culturally significant units" and how they should be incorporated into conservation biology (Laiolo & Jovani, 2007; Ryan, 2006).

Moreover, GLTs are one of the few species that potentially teach their young. In fact, they fulfil the first criterion of Caro and Hauser's (1992) definition (see Chapter 1) in two contexts: food transfers and food-offering calls (Rapaport, 1999, 2011; Rapaport & Ruiz-Miranda, 2002). However, it still remains to be investigated whether juveniles learn from the modified food transfers and food-offering calls.

### 2.6.1 Localities used in the experiments

GLTs used in the experiments came from two localities: The Poço das Antas Biological Reserve as well as one of the forest fragments located at the Fazenda Afetiva-Jorge (42º28'W, 22º37'S) (Carvalho, Nascimento, & Braga, 2006). Half of the GLT groups used in the experiments were from the Poço das Antas Biological Reserve and half were located at Fazenda Afetiva-Jorge.

Fazenda Afetiva-Jorge is also located in the municipality of Silva Jardim, Rio de Janeiro, Brazil. This area has a high density of early secondary vegetation

species, compared to the more mature forest of the Poço das Antas Biological Reserve (Carvalho et al., 2006). Despite its fragmentation, the forest at Fazenda Afetiva–Jorge is very similar in terms of species found, to the forest at the Poço das Antas Biological Reserve. This habitat corresponds to the Atlantic Forest biome, and both areas used in the study are surrounded by pasture, agricultural fields (small subsistence culture of citrus and coco fruits) and some areas of natural regeneration and secondary forest (Fazenda Afetiva-Jorge: Fig. 2.4) (Carvalho et al., 2006). The climate is similar in each, given that they are located less than 30 km apart (see Fig. 2.5), and is classified as Walter and Leith's Equatorial Type (Walter, 1971), with a mean annual precipitation of approximately 2,100 mm (Souza & Martins, 2004). There is a rainy season in the summer, with a drier period normally occurring from May to August but there is no distinct dry season (Carvalho et al., 2006). Hence although GLTs in my experiments came from two different forest areas, because of the similarity in the fauna and flora, the diet and behaviour of the GLTs are expected to be similar.

Figure 2.4: Fazenda Afetiva: cattle pasture surrounded by remnants of the Atlantic rainforest

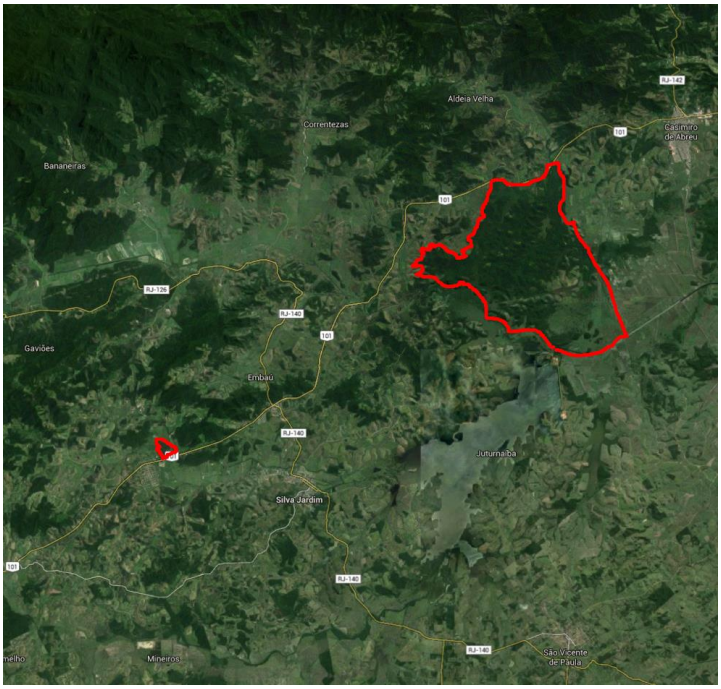


Figure 2.5: Fazenda Afetiva-Jorge on the left, and the Poço das Antas Biological Reserve on the right (Google Maps)

### 2.6.2 Golden lion tamarins studied in experiments

The individuals used in my experiments were already habituated to the presence of human observers: they do not flee when humans are approaching, are quite indifferent to human presence, and are even sometimes attracted to long-calls emitted by humans. To keep track of the population's survival, every group is monitored weekly and captured twice a year. In order to capture individuals, they are attracted to foraging platforms on which bananas are placed. But in order for GLTs not to associate humans, foraging platforms and bananas to capture events, bananas are also placed on those foraging platforms at irregular intervals when no capture events are planned. When captured, individuals are brought back to the lab at the Associação Mico-Leão-Dourado, tranquilised, and individuals are weighed, measured, individually marked with Nyanzol dye, and tattooed at birth as part of the management of the species by the Associação Mico-Leão-Dourado (Ruiz-Miranda et al., 1999). The Nyanzol markings allowed for each individual to be identifiable. Each group has a marking on a specific part of the body (e.g. right side of the head, or left leg) so that individuals belonging to different groups can be recognised. Within each group, each individual has a unique combination of markings on their tail at four

different locations: (1) where the tail connects to the body, 2) just above the midway point of the tail, 3) just below the midway point of the tail, and 4) at the tip of the tail. Hence an individual would for instance have a black dyed Nyanzol band at the very top of the tail, while another might have a black mark at the very top of the tail and just above the midway point of the tail, and another might have a mark above the midway point as well as at the tip of the tail. Some individuals had marks that were faded more than others, but generally the dye markings are reliable and allow for an easy identification of individuals. Identification of individuals was made on the video recordings, and live recording of individual presence was made during the trials to help with identification when watching the trials on video. Identification of individuals from the videos was harder when it was raining during the trials for two reasons: 1) the rain would make the GLTs' coat colour darker, so there was less contrast between the coat colour and the dye, and 2) because of the cloud cover, there was less light coming through the lens of the camera, which would also decrease the contrast between the coat and dye colour. During those rainy trials, particular care was taken to record the identity of individuals at particular time points by the human observers while trials were taking place, to help the later video analysis. This combined with deduction, made it possible to identify each marked individual. In some groups, one individual was not marked (because it avoided being trapped for a long time), however when only one individual was unmarked, it was easily identifiable. Only one group (AF2, see Table 2.2) had more than one adult individual unmarked during the second phase of the experiments; for this group it was not always possible to differentiate between the two unmarked individuals. One or two individuals of each group were also fitted with a radiotransmitter collar to allow the groups to be tracked and located through telemetry (Rapaport & Ruiz-Miranda, 2006; Ruiz-Miranda et al., 1999).

All monitored groups, which included all the groups used in my studies, were occasionally fed with bananas at trapping platforms prior to and during trapping events. When GLTs were provisioned prior to trapping events, one to three bunches of bananas were left at a foraging platform located in each group's

territory, usually when the group had been observed in the vicinity of the platform on that day. During trapping events, bananas were placed within traps, as well as openly available on the foraging platform, to attract groups to the location of the traps. Humans were always present and visible to the GLTs during trapping events, and during most provisioning events prior to trapping events. Hence human observers could have partially been associated with food provisioning, but the experiments in this thesis were not conducted when the groups were being trapped. I do not expect this habituation to have affected the results other than the GLTs being less vigilant towards humans during the experiments, as GLTs seemed unaffected by human presence. During the experiments, the human observers (a research assistant and I) were observing the trials approximately five meters away from the foraging areas, either standing or crouching depending on the vegetation cover. The observers were recording data live during the experiments, such as the presence of particular individuals, and focal sampling of juvenile behaviour, to help with the data extraction from the videos. They were therefore always visible by the GLTs, but this seemed to elicit no particular reaction from the GLTs. GLTs were usually only vigilant when humans were doing sudden movements, or sudden loud noises, so the observers during the experiments avoided those as much as possible.

Each trial in my two experiments took place between 06:30 and 12:30, which is when GLTs are most active, except for one trial that occurred in the afternoon (17:15). Every trial was recorded by two Panasonic HDC SD80 cameras, situated at approximately 45° of each other and the platform. Only the behaviour from one camera were used as data, but the second camera allowed me to double-check the behaviour from another angle, when individuals were slightly out of sight from the first camera. When the markings on the individuals' tails were hidden by a branch or other individuals on the selected videos, the second camera also helped having a second angle on the individuals to identify them more easily. The camera from which the videos were used for the data was chosen after the trials, based on which camera seemed to have a better view of the majority of the behaviour, taking into account the lighting. I coded all the

behaviour for both experiments involving GLTs, and a master's student, who was blind to the hypothesis and conditions, coded 10% of the videos to assess the consistency of the measurements and assess potential bias or measurement errors.

Table 2.2 lists all the individuals that took part in the experiments. Individuals are considered infants until they are three months of age (when they become independent of adults in terms of locomotion), juveniles are between three and nine months old (which is when they are independent of adults in terms of foraging), subadults are between nine and eighteen months old (reproductive maturity), and adults are eighteen months old and older (Rapaport & Ruiz-Miranda, 2006). I ran both experiments across two phases: the first one when juveniles were still dependent on adults (from January to March 2014), and the second one five months later (from August to October 2014), when they were considered independent (but still part of the group). When I started running trials there were 10 juveniles in six groups, which were homogenously distributed according to their sex (five females and five males). By the end of the last trials, only seven juveniles survived in five groups. Three were males and four were females. At the start of the experiments, there were also four infants that were born and survived into juvenilehood, and were therefore present during the second phase (see Table 2.2). All four infants were females. All individuals in each group were related to the breeding pair of the groups except in three of the groups where one individual was not.

Table 2.2: List of individuals that took part in the experiments (Chapter 5 and 6). Ad: adult; Sub: subadult; Juv: juvenile; Inf: infant; ABS: absent. *FA13 and FA14 were there for the first phase of the experiment in Chapter 5, but not for the first phase of the experiment in Chapter 6.

| Locality | Group | Individual | Sex | Date of Birth | Age First Phase | Age Second Phase | Present First Phase | Present Second Phase |
|---|---|---|---|---|---|---|---|---|
| Poco | BO2 | 1284 | M | - | Ad | Ad | ✓ | ✓ |
| Poco | BO2 | 1278 | F | - | Ad | Ad | ✓ | ✓ |
| Poco | BO2 | 1342 | M | 10/12 | Sub | Ad | ✓ | ✓ |
| Poco | BO2 | 1343 | M | 10/12 | Sub | Ad | ✓ | ✓ |
| Poco | BO2 | 1351 | M | 02/13 | Sub | Ad | ✓ | ✓ |
| Poco | BO2 | 1352 | F | 02/13 | Sub | Ad | ✓ | ✓ |
| Poco | BO2 | 1353 | M | 09/13 | Juv | Sub | ✓ | ✓ |
| Poco | BO2 | 1354 | F | 09/13 | Juv | Sub | ✓ | ✓ |
| Poco | AF | FA3 | M | 10/09 | Ad | Ad | ✓ | ✓ |
| Poco | AF | AF13 | F | 12/08 | Ad | Ad | ✓ | ✓ |
| Poco | AF | AF19 | M | 10/11 | Ad | ABS | ✓ | |
| Poco | AF | AF20 | F | 12/11 | Ad | Ad | ✓ | ✓ |
| Poco | AF | AF35 | M | 12/12 | Sub | Ad | ✓ | ✓ |
| Poco | AF | AF27 | F | 10/13 | Juv | Sub | ✓ | ✓ |
| Poco | Alone | 1303 | M | - | Ad | Ad | ✓ | ✓ |
| Poco | Alone | 1313 | F | 11/09 | Ad | ABS | ✓ | |
| Poco | Alone | 1360 | F | - | ABS | Ad | | ✓ |
| Poco | Alone | 1355 | M | 10/13 | Juv | Sub | ✓ | ✓ |
| Poco | Alone | 1356 | M | 10/13 | Juv | ABS | ✓ | |
| Afetiva | AF2 | SP6 | M | 10/06 | Ad | Ad | ✓ | ✓ |
| Afetiva | AF2 | AF4 | F | 10/04 | Ad | Ad | ✓ | ✓ |
| Afetiva | AF2 | BE1 | M | 01/02 | Ad | Ad | ✓ | ✓ |
| Afetiva | AF2 | FA6 | F | 10/10 | Ad | Ad | ✓ | ✓ |
| Afetiva | AF2 | FA8 | M | 10/11 | Ad | Ad | ✓ | ✓ |
| Afetiva | AF2 | FA10 | M | 10/2 | Sub | Ad | ✓ | ✓ |
| Afetiva | AF2 | FA11 | M | 10/12 | Sub | Ad | ✓ | ✓ |
| Afetiva | AF2 | FA12 | F | 10/12 | Sub | Ad | ✓ | ✓ |
| Afetiva | AF2 | FA13 | M | 09/13 | Juv | ABS | ✓* | |
| Afetiva | AF2 | FA14 | F | 09/13 | Juv | ABS | ✓* | |
| Afetiva | AF2 | FA15 | F | 02/14 | Inf | Juv | ✓ | ✓ |
| Afetiva | AF2 | FA16 | F | 02/14 | Inf | Juv | ✓ | ✓ |
| Afetiva | AF3 | PT8 | M | 10/01 | Ad | Ad | ✓ | ✓ |
| Afetiva | AF3 | SP18 | M | 10/09 | Ad | Ad | ✓ | ✓ |
| Afetiva | AF3 | FA2 | F | 12/08 | Ad | Ad | ✓ | ✓ |
| Afetiva | AF3 | FP1 | M | 12/12 | Sub | ABS | ✓ | |
| Afetiva | AF3 | FP2 | F | 12/12 | Sub | Ad | ✓ | ✓ |
| Afetiva | AF3 | FP3 | F | 09/13 | Juv | Sub | ✓ | ✓ |
| Afetiva | AF3 | FP4 | M | 09/13 | Juv | Sub | ✓ | ✓ |
| Afetiva | Super | SP16 | F | 11/08 | Ad | Ad | ✓ | ✓ |
| Afetiva | Super | FA4 | M | 10/09 | Ad | Ad | ✓ | ✓ |
| Afetiva | Super | SP20 | M | 11/11 | Ad | Ad | ✓ | ✓ |
| Afetiva | Super | SP23 | F | 12/12 | Sub | Ad | ✓ | ✓ |
| Afetiva | Super | SP24 | F | 12/12 | Sub | Ad | ✓ | ✓ |
| Afetiva | Super | SP25 | F | 12/12 | Sub | ABS | ✓ | |
| Afetiva | Super | SP26 | F | 09/13 | Juv | Sub | ✓ | ✓ |
| Afetiva | Super | SP27 | F | 02/14 | Inf | Juv | ✓ | ✓ |
| Afetiva | Super | SP28 | F | 02/14 | Inf | Juv | ✓ | ✓ |

## 2.7 Ethical note

Both experiments in this thesis regarding golden lion tamarins were performed in accordance to the guidelines of the Association for the Study of Animal Behaviour (ASAB) and were approved by the Animal Welfare and Ethics Committee of the University of St Andrews. Ethics was also approved by ICMBio for project number 17409-9 and 17409-12, "Manejo de metapopulação do mico-leão-dourado: pesquisa e ações". See Appendix 2.A.

# Chapter 3:

# The ecology, behaviour and social learning abilities of the domestic fowl

## 3.1 Abstract

In this chapter, I will give a short introduction to domestic fowl (*Gallus gallus domesticus*), highlighting similarities with the red junglefowl (henceforth RJF) (*Gallus gallus gallus*), their non-domesticated counterpart. I will discuss some aspects of their ecology, social structure and general behaviour. Finally, I will describe their maternal behaviour and review experimental evidence of social learning in both species, two aspects which are particularly relevant to the experiment reported in this thesis.

## 3.2 The red junglefowl and the domestic fowl

### 3.2.1 Ecology

The domestic fowl is one of the most widespread domestic animals. It is derived from one or several subspecies of the red junglefowl. Evidence suggests that this domestication happened over 8,000 years ago (see Nicol, 2004).

The RJF is mainly found in Asia: according to Delacour (1951) they range from northeast and central India, extreme southern China and southeast Asia, to Sumatra, Java and Bali. RJFs live in brush and forest environments (McBride, Parer, & Foenander, 1969) and will eat a variety of food: insects, spiders, snails, earthworms, lizards, leaves, petals, grass and seeds, rice, bamboo, fruits, and roots (Collias & Saichuae, 1966). Predators include hawks, eagles and cats [fishing cats (*Prionailurus viverrinus*) and palm civet (*Paradoxurus hermaphroditus*)] (Collias & Saichuae, 1966).

### 3.2.2 Social structure

RJF live in harem-polygynous societies, where mixed-sex flocks comprise 4 to 30 adults (McBride et al., 1969; Mench & Keeling, 2001), although lone males or females are not uncommon (Collias & Saichuae, 1966). Males are often seen alone, especially when competing for mates, whereas hens are more rarely seen in isolation (Collias & Collias, 1967). Within flocks, a dominant male will

guard the group (McBride et al., 1969) and will be the most dominant individual in the group (Daisley, Rosa Salva, Regolin, & Vallortigara, 2011). However, males and females form two separate dominance hierarchies (Wood-Gush, 1971).

In males, body size, degree of pigment saturation, and comb size are all significantly correlated with dominance (Ligon, Thornhill, Zuk, & Johnson, 1990; Zuk, 2000). In fact, combs are strongly affected by levels of testosterone in the blood, and also reflect the physical condition of individuals (Ligon et al., 1990). Agonistic behaviour plays an important role in courtship (Kruijt, 1964), and as a result, dominant cocks mate with more than twice as many hens as do subordinate cocks (Collias & Collias, 1996),

Hens within the harems also have a dominance hierarchy, which is very stable over time (Banks, 1956; Mench & Keeling, 2001), and which becomes established around 8 to 10 weeks of age (Guhl, 1958). The hierarchy is based on physical attributes, hormonal status and agonistic interactions such as pecking and threats (Mench & Keeling, 2001). Although the hierarchy is established mainly through agonistic interactions, it is maintained through dominance displays (Daisley et al., 2011). In response to displays, subordinate hens increase their distance from dominant hens (Banks, 1956). The dominance hierarchy will determine which individual feeds first, roosts and nests in the best position, and potentially gains access to more mates (Daisley et al., 2011). More dominant hens raise more chicks to independence over the course of their lifetime and hence have higher reproductive success than subordinate hens (Collias & Collias, 1996; Collias, Collias, & Jenrich, 1994).

The dominance hierarchy observable in RJF and domestic fowl implies that individuals recognise each other and have learned the relationships between individuals (Wood-Gush, 1971). In fact, domestic fowl are able to perform transitive inference, and will respond appropriately after having observed interactions between pairs of individuals (Hogue, Beaugrand, & Laguë, 1996).

### 3.2.3 General behaviour

#### 3.2.3.1 Foraging behaviour

Hens spend the majority of their time foraging: they spend 60% of their active time ground pecking and 34% of their active time ground scratching (Dawkins, 1989). Ground pecking behaviour is present immediately after hatching and ground scratching is observed from day 3. Chicks first start pecking at food and non-food alike, so have to learn which food they should ingest (Hogan, 1984). However, the tendency in Burmese RJF chicks to peck at inedible objects remains throughout their life (Kruijt, 1964).

Food calls are also often emitted in association with foraging behaviour and are usually dependent on the presence of food, with call rate correlating with food quality or preference (Wauters & Richard-Yris, 2002; Wauters, Richard-Yris, Pierre, Lunel, & Richard, 1999). However food calls can also be modulated by the social context (Evans & Evans, 1999; Marler, Dufty, & Pickert, 1986b). In fact, food calls play an important role in both courtship and parental behaviour of gallinaceous birds (Kruijt, 1964; Moffatt & Hogan, 1992; Stokes, 1971). In courtship display, cocks use the tidbitting display [a multimodal signalling display that comprises of food calls and a distinctive visual display (Evans & Marler, 1994; Stokes & Williams, 1972)] to attract a hen to their location. As part of the parental behaviour, hens also attract chicks to the location where they had been eating, also with food calls. Males emit food calls when both food and hens are present, and hens emit them when both food and chicks are present (Evans & Marler, 1994; Marler et al., 1986b; Sherry, 1977). However, food calls are also sometimes emitted in the absence of food (Gyger & Marler, 1988; Hughes, Hughes, & Covalt-Dunning, 1982).

#### 3.2.3.2 Social behaviour

Domestic fowl and RJF are very social species. Hens prefer to be in contact with familiar individuals rather than unknown hens (Bradshaw, 1992), and young chicks start aggregating at an early age (Wood-Gush, 1971). Experimental

studies have shown that social experience with conspecifics leads to the formation of normal patterns of aggregation in domestic fowl, but this social experience does not have to be introduced at the start of life: social exposure later in life mitigates the effect of isolation in chicks, suggestive that there is no critical period (Baron & Kish, 1960). Baron and Kish's (1960) experiment also suggests that aggregative behaviour is a result of learning resulting from social interaction, which, unlike imprinting, is not restricted to a single period in early life.

Vocal communication is also an important part of the fowl's social behaviour. In fact, domestic fowl have at least 31 different calls through which they communicate with other individuals about food or predators (Evans & Evans, 1999; Evans & Marler, 1994; Wood-Gush, 1971).

### 3.2.4 Similarity between domesticated fowl and red junglefowl

Despite domestication occurring thousands of years ago, experimental investigations have established relatively few differences between the behaviour of feral domesticated fowl and RJF (Nicol, 2004). A number of studies have systematically evaluated the behavioural time budgets in domestic fowl and RJF. All behaviousr observed in RJF are present in domestic fowl (Wood-Gush & Duncan, 1976), and both wild and domesticated fowl were found to assess costs and benefits of a foraging situation similarly, and behave according to optimal foraging theory (Andersson, Nordin, & Jensen, 2001). Both domesticated fowl and RJF also respond similarly to simulated predator attacks with a decrease in food pecking and an increase in walking behaviour (Schütz, Forkman, & Jensen, 2001). Regarding the social organisation (Banks, 1956; Collias & Collias, 1996; McBride et al., 1969) and social patterns (Kruijt, 1964; Wood-Gush, 1971) of small flocks of hens, there is no essential difference between domestic hens and wild RJF. The two sub-species have very similar social behaviour, except for a few changes in frequency and intensity of behaviour (Väisänen, Håkansson, & Jensen, 2005). Small behavioural differences were indeed noted in several studies, which could be the result of a reduction of natural selection pressures in

the domesticated populations (Andersson et al., 2001). For instance, Leghorns, a breed of domesticated fowl, were found to be more cohesive in their spacing pattern than RJF (Väisänen et al., 2005). They were also more aggressive and had more sexual interactions than RJF (Väisänen et al., 2005), but RJF were more exploratory and expressed more foraging behaviour than Leghorns (Väisänen & Jensen, 2003). Another study reported that Leghorns adapt to new environments more effectively compared to RJF, a finding possibly influenced by selection for increased production capacity (Väisänen & Jensen, 2003).

It has also been noted that social behaviour differs to some degree between domestic fowl breeds (Craig & Muir, 1996; Guhl, Craig, & Mueller, 1960; Hocking, Channing, Waddington, & Jones, 2001; Jones, Marin, Garcia, & Arce, 1999). However, the effect of domestication on the social behaviour of domestic fowl is generally thought to be more quantitative than qualitative, with differences mainly in the frequencies and intensities of behaviour, rather than distinctively different behaviour (Mendl & Held, 2001; E. O. Price, 1998; Väisänen et al., 2005).

### 3.3 Maternal behaviour

Hens' broodiness is characterised by specific attributes: non-aggressiveness towards chicks, warming of chicks through prolonged contact ("brooding") and emissions of maternal calls, principally clucks and tidbitting calls (Richard-Yris, Leboucher, Chadwick, & Garnier, 1987). This allows strong social attachments between chicks and hens to be formed early in life (Baron & Kish, 1960). Under natural conditions, the contact between a mother hen and her chicks (both domestic fowl and red junglefowl) lasts for a long time, for example up to 5 to 12 weeks in *Gallus gallus spadiceus* (McBride et al., 1969; Perré, Wauters, & Richard-Yris, 2002).

In birds, the effects of parental contact have mainly been investigated in the context of studies of imprinting and song learning, but there are also well-established parental effects on sexual behaviour, feeding behaviour, and aggressive behaviour (see Perre et al., 2002). In domestic fowl, the presence of a

mother hen during development leads to pullets being less neophobic when approaching a novel object and more explorative of their environment compared to pullets raised in their mother's absence (Perré et al., 2002). Brooded pullets also tend to seek the proximity of conspecifics, but are more aggressive towards unfamiliar conspecifics than pullets that were not brooded (Perré et al., 2002). Hence, the influence of the presence of a mother during development is still detectable after the end of maternal contact (Perré et al., 2002). Perré et al. (2002) also suggest that the presence of social partners other than the mother can have important impacts on the development of young chicks.

### 3.3.1 Recognition

Several experiments have shown the importance of visual and auditory stimuli on the development of a strong relationship between hens and their chicks (Kent, 1987). For instance, chicks can discriminate between their mother hen and other familiar hens based on cluck vocalisation, but are only able to do so if social contact is maintained constantly (Kent, 1987). After four hours of separation, chicks fail to discriminate between their mother and familiar hens during live demonstration (which would entail a combination of visual, auditory and olfactory cues)(Kent, 1987). This shows that filial imprinting can be reversed. On top of auditory stimuli, chicks also use visual stimuli to recognise the hen (Collias, 1952). In contrast, there is little evidence that hens recognise their chicks (Collias, 1952; Wood-Gush, 1971), although hens will reject an experimentally introduced chick if it is of a different age than that of their chicks (Brückner, 1933; cited in Sherry, 1977).

### 3.3.2 Maternal food display

Young chicks do not have an unlearned capacity to recognise edible from inedible food (Hogan, 1984): rather, learning seems important in this species to acquire appropriate foraging behaviour (Nicol, 2004, 2006). Moreover, ingestion is not strongly involved in the pecking motivation of chicks (Hogan, 1984). Young chicks have been found to be more attentive to the behaviour of conspecifics of the same age than to an older conspecific (Nicol, 2006). Burmese

RJF and domestic fowl have a similar display when they attract young to food (Stokes, 1971). When discovering food, a broody hen will inhibit eating and emit food calls, distinctive as a rapid staccato call *"consisting of a series of pulses delivered at a rate of 5 to 7 pulses per second*" (Sherry, 1977, p. 594). They will also adopt a specific posture where the hen will "*pivot forwards and with the back steeply inclined, the breast close to the ground and the tail raised and open, peck at the food, pick it up and drop it repeatedly, peck the ground and peck vigorously with the food held in the bill*" (Sherry, 1977, p. 594). On top of this display, a hen will pick up and drop food and let chicks take food from her beak (Sherry, 1977; Stokes, 1971). This combination of behaviour will alert chicks to the presence of food. In a semi-wild population, Stokes (1971) also found that nearly half of the hens acquired a male consort to help her feed the chicks. Hence hens have developed several techniques to insure chicks obtain food. Other gallinaceous birds, such as the white-tailed ptarmigan, have a multimodal tidbitting display that is similar to that of domestic fowl and the RJF (Clarke, 2010). White-tailed ptarmigans also use food calling to stimulate their chicks to join them in consuming preferred plants (Clarke 2001). Clarke (2010) further suggest that white-tailed ptarmigans might teach their young to feed on plants containing high levels of proteins by influencing the chicks' diet.

Hens also express their foraging preference with increased food calls (Wauters et al., 1999). Hens deliver food calls more rapidly when encountering higher quality food compared to poorer food, and these food calls also have more notes compared to a food call indicating a lower quality food (Marler, Dufty, & Pickert, 1986a).

### 3.3.3 Responses of chicks to maternal food display

Chicks respond to the maternal display by approaching the hen, increasing their pecking behaviour, and pecking at the same object the hen is pecking at as well as pecking at the tip of the hen's beak (Stokes, 1971; Wauters & Richard-Yris, 2002). Chicks are attracted to this multimodal display, which combines pecking sounds and movement of their mother. The chicks' response is enhanced

by the emission of food calls by the hen (Turner, 1964; Wauters, Richard-Yris, & Talec, 2002). Chicks increase their pecking behaviour when food calls are present compared to when they are not (Wauters & Richard-Yris, 2002). When a display sequence containing food calls is produced by hens, chicks are more likely to begin or change their feeding activity than when no food calls are emitted (Wauters & Richard-Yris, 2002). Chicks also respond faster to calls of high quality food compared to calls of low quality food, but only if those are reinforced appropriately: if, after a high-quality food call, the chicks obtain low-quality food, chicks will start responding equally to high- and low-quality food calls (Moffatt & Hogan, 1992). Hence the hen's behaviour is important in encouraging chicks to peck at edible items (Nicol, 2004). Moreover, with natural food calls chicks respond faster as they grow older, indicating that they probably learn the association between food calls and presence of food (Wauters & Richard-Yris, 2002).

The mere presence of another conspecific, either same-aged chicks or the mother, has also been found to increase pecking activity in chicks (Tolman & Wilson, 1965; Wauters et al., 2002). However, the mothers' display further directs the foraging behaviour of chicks.

### 3.3.4 Flexibility of the maternal food display

Although the presence of both food and chicks are usually required for hens to emit food calls, hens are flexible in the way they use food calls and will adapt to the social context. For instance, Sherry (1977) found that the sight of chicks inhibits hens from feeding and prolongs their display. Visual, but not auditory stimuli of chicks lead to feeding inhibition by the hen and prolongs food calling. However, the loss of both vocal and auditory contact will also prolong the display (Sherry, 1977). Moreover, hens emit more food calls when their chicks have been at some distance for several seconds (Stokes, 1971; Wauters & Richard-Yris, 2002) or when they fail to respond to the hen's display (Stokes, 1971) than when they are close and responsive. The hen's display is also increased when the chicks are in sight but are physically separated from her compared to when they

are free to interact with the hen (Wauters et al., 1999). Hens will emit louder calls if their chicks are far away compared to close (Wauters et al., 1999). Such food calls could function to gather the brood, as the intensity of the food call increases with the distance between chicks and hens (Sherry, 1977; Stokes, 1971). In sum, hens are sensitive to their chicks' proximity: the further the chicks, the louder, faster and longer the food call emitted by the hen (Stokes, 1971).

Wauters and Richard-Yris (2002) also showed that when pecking, hens emit more food calls when their chicks are not feeding than when they are feeding. Hens not only react to the distance between themselves and their chicks, but also to the intensity of the chicks' feeding behaviour, which also seems to stimulate the hens' vocalisations (Wauters & Richard-Yris, 2002). A further experiment established that hens were sensitive to whether the behaviour of their chicks was in concordance with their own knowledge (based on their prior experience) (Nicol & Pope, 1996). This suggests that the hen's display might not only attract chicks to palatable food but could also discourage the chicks from consuming unpalatable good (Nicol & Pope, 1996). In would seem that hens respond flexibly to the chicks' behaviour, potentially to teach them foraging preferences (Nicol, 2004, 2006).

Overall, mothers modify their behaviour based on both the chicks' presence and behaviour. As chicks grow older, the number of displays by hens in which there are food calls, and the number of food calls decrease (Wauters & Richard-Yris, 2002).

## 3.4 Social learning

### 3.4.1 Social learning in chicks

Several studies suggest that social learning plays an important role in the development of the young, and in the acquisition of food preferences in juvenile birds (Moffatt & Hogan, 1992; Sherry, 1977; Stokes, 1971). For many young the parents will provide the most important source of information (Nicol, 1995), and

maternal deprivation in commercial farms has welfare implications (Edgar, Held, Jones, & Troisi, 2016). As seen previously, there is strong evidence that the maternal display of the hen influences the foraging decisions of young chicks (domestic and RJF) (Nicol, 2004, 2006) and chicks are known to follow their mothers' foraging preference (Moffatt & Hogan, 1992; Nicol & Pope, 1996; Sherry, 1977; Stokes, 1971; Wauters & Richard-Yris, 2002; Wauters et al., 2002) (and Allen & Clarke (2005) in white-tailed ptarmigans). Domestic chicks hatch with sufficient spare yolk to last approximately four days without eating (Romanoff, 1944). This gives chicks four days to learn to discriminate between edible and inedible objects (Suboski & Bartashunas, 1984). Although young are precocial, they typically require at least one parent to be present to help them to obtain food in the first few weeks of life (Stokes, 1971). However, while several experiments show evidence of an immediate response of the chicks to the mother's foraging behaviour, and social learning from chicks to chicks and from artificial hens or arrow models to chicks, it still remains to be shown that chicks learn foraging preferences from hens. Further details on social learning in young chicks are presented in Chapter 7, particularly section 7.2.1.

Acquiring foraging information as to what food is good to eat is crucial for young chicks, as making the wrong choice can be dangerous. Moreover, chicks peck at both edible and inedible particles alike (Hogan, 1984). Hence there might be a selection pressure for teaching to evolve. Moreover, young chicks are capable of social learning, suggesting that some mechanisms are already in place for teaching, particularly in the learner's side. However, acquiring this social information during foraging decisions is not particularly costly or difficult, at least in the domestic fowl, as chicks are easily able to follow the hen wherever she goes, and resource limitation is not usually an issue. Hence, whether there are enough selection pressures in this species for teaching to evolve can be questioned. There is likely to be more selection pressure for teaching in their wild counterparts, the red jungle fowl, due to the habitat structure and resource availability.

### 3.4.2 Social learning in adults

There is evidence that social learning in adult hens and chicks is different (Johnston, Burne, & Rose, 1998; Nicol & Pope, 1992; Sherwin, Heyes, & Nicol, 2002; Suboski & Bartashunas, 1984). For instance, although there have been reports of one-day-old and two-day-old chicks avoiding food following a conspecific's disgust reaction (Johnston et al., 1998; Salva, Daisley, Regolin, & Vallortigara, 2009), this avoidance is not present in older individuals (Sherwin et al., 2002). This suggests that the use of social information varies with the age of domestic fowl. However, the study with older individuals reported considerable individual variation in responses, and hens that showed a disgust reaction still continued pecking at the unpalatable food, potentially sending conflicting information to observer hens (Nicol, 2004).

Nonetheless, extensive experimental evidence suggests that older conspecifics influence each others' foraging choices (Gajdon, Hungerbuhler, & Stauffacher, 2001; McQuoid & Galef, 1992, 1993, 1994, Nicol & Pope, 1992, 1993, 1994, 1999; Sherwin et al., 2002). In the aforementioned Sherwin et al. (2002) experiment with older hens, the demonstrators' pecking rate was positively correlated with the proportion of food of the demonstrated colour pecked at by the observer bird (but only if the food was red). Red food is usually avoided, so this demonstration could prevent hens from avoiding particular coloured food. Hence, nine-week-old pullets were found to eat a coloured food that they would usually avoid, after observing a conspecific peck at the same colour (Sherwin et al., 2002). On the other hand, when hens observed the demonstrator in the vicinity of a coloured food but without seeing pecking, they later avoid pecking at this food (Sherwin et al., 2002). This does not seem to be the case in young chicks, as there is little evidence showing that chicks inhibit pecking at objects that have been avoided by others (Johnston et al., 1998). Hens are therefore sensitive to the pecking frequency of the demonstration towards palatable food. In fact, when a hen encounters highly palatable or preferred food, she will increase the pecking and scratching rate in an "*excited manner*", which usually

attracts the attention of conspecifics who will approach the hen (Sherwin et al., 2002, p. 934).

Further social learning experiments in a foraging context have shown that RJF show feeding site preference and shorter latency to feed if they have previously observed a conspecific forage successfully from that site 48h before compared to alternative feeding sites (McQuoid & Galef, 1992, 1993). Similar findings were shown with video demonstrations (McQuoid & Galef, 1993). In order for observers to learn, McQuoid and Galef (1992) point to the importance of seeing a demonstrator with a reward.

There is also evidence of social transmission of key pecking to obtain food rewards in domestic hens (Nicol & Pope, 1992, 1993, 1994, 1999). Nicol and Pope (1992) also showed that although there was social transmission of information between a real demonstrator and the observer, this did not occur when the demonstrator was an artificial rod simulating pecking movements. Hence there is something specific about the behaviour of the demonstrator that facilitates the acquisition of the response in the observer (Nicol & Pope, 1992). Similar social transmission of pecking preferences is also observed in small flocks rather than with a one-demonstrator-one-observer paradigm (Nicol & Pope, 1994).

Social transmission of cannibalistic behaviour has also been demonstrated in hens (Cloutier, Newberry, Honda, & Alldredge, 2002). Cloutier et al. (2002) showed that pairs that had observed a demonstrator pierce a membrane containing conspecific blood and consuming it were more likely to do the same thing when the demonstrator was removed than control pairs that had not observed a demonstrator perform the action. Moreover, there is suggestive evidence that social learning could play a role in the spread of feather pecking behaviour (Zeltner, Klein, & Huber-Eicher, 2000). Chicks in groups where feather-pecking chicks were introduced had significantly higher rates of feather pecking compared to chicks in groups where control chicks were introduced

(Zeltner et al., 2000). Social learning therefore has important implication for welfare regarding the spread of harmful behaviour.

Overall, the importance of social learning seems to vary with the domestic fowl's age (Nicol, 2006). In her review, Nicol (2004) states the belief that young birds primarily establish food preferences through social influences (although as noted above, it still remains to be shown whether chicks learn from hens). In older birds, other factors such as a social dominance and stimulus colour interact with social learning to influence the acquisition of new food or stimulus preferences.

### 3.4.3 Effect of dominance on social learning

When investigating social learning in adult hens, experiments report evidence of an effect of hierarchy and the status of the demonstrator. There is evidence that the social transmission of food preferences is greater when the demonstrator is socially dominant compared to socially subordinate demonstrators or unfamiliar demonstrators (Nicol & Pope, 1994, 1999). Dominant hens could receive more attention from conspecifics because they pose more of a threat or because they are more successful in other domains (Nicol, 2004; Nicol & Pope, 1994). For instance, dominant RJF have a higher reproductive success than subordinate RJF (Collias et al., 1994). However, in an experimental manipulation, Nicol and Pope (1999) found no effect of manipulating the prior foraging success of individuals on their likelihood of being copied. However, hens were also more successful at pecking at a key when they had observed a dominant hen peck at the key compared to a subordinate hen or a cockerel pecking at the key (Nicol & Pope, 1999). Cockerels are dominant over hens, suggesting an interaction between dominance and sex with respect to demonstrators' influence on foraging (Nicol & Pope, 1999). The individual towards which the observer pays more attention is not predicted by the demonstrator's pecking rate or accuracy (Nicol & Pope, 1994), nor by body size or force of key pecking, since very little social learning resulted from observing cockerels (Nicol & Pope, 1999). Individuals may pay more attention to

dominant individuals because of a fear of aggressive behaviour, and they have more to fear from a dominant hen than a cockerel, even if the cockerel is more dominant (Nicol & Pope, 1999). However, Gajdon et al. (2001) found that young chicks learn more from chicks of similar age than from chicks that are three days older than them. The authors suggested that the aggressive behaviour shown by older chicks decreases the focal chick's focus on the foraging behaviour being demonstrated. Hence it is unclear what individuals pay attention to when they observe dominant individuals.

On the other hand, Croney et al. (2007) examined the role of dominance in social learning, but found no difference in performance of dominant and subordinate birds in a visual discrimination task. This suggests that subordinate birds are not better at social learning than dominant birds, and that there must be some perception bias towards dominant hens.

### 3.4.4 Effect of food deprivation on social learning

In many social learning of foraging information experiments individuals are food deprived, based on the assumption that the birds' motivation to acquire food, and therefore to use social information, will increase with hunger level. However, while examining the effects of food deprivation on social learning, Nicol and Pope (1993) found that, contrary to expectations, non-deprived birds pecked more and preferentially towards the demonstrated key, compared to food-deprived birds. These authors suggested that food-deprivation has an inhibitory effect on subsequent behaviour and leads birds to be less attentive to the details of the demonstration. Food deprivation could therefore have a contradictory effect on attention.

### 3.4.5 Effect of access to demonstrator on social learning

In chicks, having direct access to the demonstrator chick enhances social learning, compared to when chicks have restricted access to their demonstrator, but can fully observe them (Gajdon et al., 2001). In both situations, however, social learning can occur. On the other hand, in adult hens, having access to the

demonstrator and the stimulus reduced social learning in a key pecking experiment where pecking on keys would give to access to a reward (Nicol & Pope, 1994). This could be because of increased aggression amongst adults, since Nicol and Pope (1994) saw that the demonstrator would either prevent observers having access to the stimulus by guarding it, or the demonstrator was chased from the stimulus by other hens, and therefore no demonstration ensued. The Gajdon et al. (2001) and Nicol and Pope (1994) studies further highlight changes in the pattern of social learning with the age of individuals. Cloutier et al. (2002) showed that when social learning did not lead to access to a reward, direct access to the stimuli, rather than only observation of the behaviour, increased the transmission of the behaviour for cannibalistic behaviour.

## 3.5 This study

There is considerable evidence of social influence and social learning in RJF and domestic fowl, particularly in the context of foraging behaviour. Young chicks' foraging behaviour is influenced by the hen, and later by conspecifics within their group. Observers learn more from watching a dominant than a subordinate individual. Social learning in domestic fowl is therefore not fixed, but depends on the context and social relationship between the observer and demonstrator (Nicol, 2006). However, there is still no evidence that chicks learn which food to eat from their mother, and there is still sparse knowledge about the mechanisms underlying social transmission of information in those species.

Of particular relevance to this thesis is the observation that fowl are one of the few species that potentially teach their young. Fowl fulfil the first criteria of Caro and Hauser's (1992) definition in a foraging context (see Chapter 1) (Nicol & Pope, 1996). There is also suggestive evidence of teaching behaviour in a closely related species, the white-tailed ptarmigan (Allen & Clarke, 2005; Clarke, 2010). However, it still remains to be investigated whether juveniles learn from the modified foraging display of their mothers and for how long they might retain that knowledge. This question is addressed by the experiment presented in Chapter 7.

## 3.6 Ethical note

The experiment in this thesis regarding domestic fowl was performed in accordance to the guidelines of the Association for the Study of Animal Behaviour (ASAB) and was approved by the Ethical Review Group of the University of Bristol (University Investigation Number: UIN/13/031, project: "Teaching behaviour in broody hen").

# Chapter 4:

# General statistical methods

In this chapter, I will introduce and describe the different statistical approaches used in each experiment, as well as the philosophy underlying those approaches. All analyses were carried out in the R statistical environment version 3.2.1 (R Development Core Team, 2015) and the package *pastecs* (Grosjean & Ibanez, 2014) was used to obtain descriptive statistics.

## 4.1 Chapter 5: Role of food transfers in wild lion tamarins: evidence for teaching behaviour?

### 4.1.1 First phase

In the first phase of this experiment, I used a series of generalised linear mixed models (GLMMs) to ask the following questions:

1) Are novel food transferred more successfully than familiar food?
2) Are juveniles more likely to attempt to obtain novel food from other individuals, compared to familiar food?
3) Are adult donors more likely to resist a food transfer of novel food, compared to a transfer of familiar food?
4) When the donor is resisting the food transfer, are juveniles more successful in obtaining novel foods compared to familiar foods?

GLMMs allow for the inclusion of random factors, and therefore provide a mean for dealing with non-independence of the data (Grueber, Nakagawa, Laws, & Jamieson, 2011). Random effects for receiver and donor individuals were added to all analyses (unless specified), allowing for within individual correlations in propensity to obtain or give up food, respectively. I also included a further random effect for the group to which the individuals belonged (individuals nested in groups), to allow for within group correlations. Thus the models reduced the possibility that extreme individuals or groups might disproportionately influence estimates of the effects. In all cases I used a binomial error structure and logit link function, using the glmer function in the *lme4* package (D. Bates, Maechler, Boler, & Walker, 2015). More details for each analysis are provided in Chapter 5 (5.3.7.1).

Although food familiarity was my main factor of interest when looking at the individuals' decisions, there are many other predictor variables linked to the individuals or their experience with the food that could also have had an impact on the observed behaviour. In order to determine the relative importance of the predictor variables in each model, I used an information-theoretic approach with model-averaging as described in Grueber et al. (2011). With this approach, a series of candidate models was generated. Each of them represented a biological hypothesis. Hence, instead of testing a null hypotheses, as with the frequentist approach, here, I examined several hypothesis at the same time, and identified the ones that best fitted the data (Burnham & Anderson, 2002). This led to calculating the relative degree of support for each model (and hypothesis) in the candidate set (Burnham & Anderson, 2002). First, a global model, including all of the predictor variables and random effects, was specified. For each analysis, the global model included parameters relevant to the food novelty which was the main factor of interest, as well as parameters relevant to the individuals (age and sex) and the individuals' previous experience with the food during the course of the experiment. Parameters relevant to the individual donors and receivers, such as age and sex, were included because of previous findings. In fact, it is known that transfers occur mainly towards juveniles and pregnant females, and in some species it is also known that the father is more involved in the food transfers towards its offspring (Feistner & Chamove, 1986; Moura et al., 2010; E. C. Price & Feistner, 1993; Rapaport, 1999, 2006; Ruiz-Miranda et al., 1999). Only when the data were restricted to transfers from adults to juveniles were the individuals' age not included as parameters.

For each of the question of interest, because of the number of parameters, the model sets were large. The model averaging approach was therefore used to account for model selection uncertainty (Grueber et al., 2011). The dredge function from the *MuMIn* package (Bartoń, 2016) was used to conduct this model averaging. This compared all of the submodels from the initial global model. The model comparison was done using the Akaike Information Criterion corrected for small sample sizes (AICc) (Bartoń, 2016). The AIC is an index that takes into account the likelihood of the model as well as the number of parameters in that

model (through parsimony), and ranges between zero and one (Nakagawa & Cuthill, 2007). By using AICs, issues related to conventional p-values, such as an arbitrary threshold, are avoided (Grueber et al., 2011). Moreover, by penalising the model for the number of parameters, this approach minimised the number of falsely positive predictors that were included in each model (Waite & Campbell, 2006). The model with the smallest AIC is supposed to retain all of the important predictors (Nakagawa & Cuthill, 2007). However if the first ranked model's weight is different from one, there is uncertainty about which model is the best (Burnham & Anderson, 2002; Grueber et al., 2011). In this case, interpretation should rely on a set of models, rather than just the best model (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). Hence following Grueber et al.'s (2011) methodology, the set of "top" models was defined by taking the best model (the model with the lowest AICc value) and all the other models that were within two AICc units of the best model (Burnham & Anderson, 2002). Models within two AICc of the top model were considered to be as informative as the top model (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). Here I used the full-model averaging approach, where the inference is based on all models in the candidate set, because of the high model uncertainty observed (when the best AICc is not strongly weighted) (Symonds & Moussalli, 2011). With the top models, the averaged parameter estimates for each predictor variable as well as their relative importance, were computed. The relative importance is calculated by summing the Akaike weights of all models where the predictor variable in question is present. Akaike weights represent the probability of a given model to being the best model compared to other models in the subset (Burnham & Anderson, 2002). The relative importance of a variable can therefore be thought of as the probability that this particular variable is part of the best model (Symonds & Moussalli, 2011). However, it is not the probability that the variable has a statistical effect (Galipaud, Gillingham, David, & Dechaume-Moncharmont, 2014). On top of the relative importance of the predictors present in the top models (those within two AICc units of the best model), the result section of the first phase of the experiment in Chapter 5 (5.4.1) reports the parameter estimates, their standard errors, and their 95% confidence intervals as well as the back-transformed effect on odds and their 95% confidence intervals

(Galipaud et al., 2014). Standard errors are unconditional, meaning that they incorporate model selection uncertainty.

The information-theoretic approach with model averaging was used as it allows ine to compare several competing models (i.e. hypotheses) simultaneously and make inferences based on the weighted support for several models (Grueber et al., 2011). Model averaging also allows one to reduce model uncertainty, compared to stepwise methods of model selection (Grueber et al., 2011).

### 4.1.2 Second phase

In the second phase of this experiment, in order to predict the foraging choices made by juveniles I used Bayesian statistics, using the *rstan* package (Stan Development Team, 2015) and the *rethinking* package (McElreath, 2015). Unlike null hypothesis testing, the Bayesian approach allows one to calculate the probability of a given hypothesis given the data (Nakagawa & Cuthill, 2007). Within this Bayesian framework I used the softmax function to model individual decisions, because multiple choices were available. The softmax function is a logistic function that gives the probability for each of multiple possible actions occurring. Once it knows what the action was (data from the first trial of the second phase) the algorithm used this to calculate the likelihood of that action having occurred given the model parameters. In fact, it converted attraction scores for multiple options to a range between zero and one, so that the softmax value (probability) for all of the actions added up to one. In my data, I was interested in modelling the decision of juveniles eating a particular food type based on this softmax function. Hence the numerator is the chosen food type and the denominator the sum over all food types. The softmax function makes the attraction score of the chosen food type relative to those of other food types:

$$L = Pr(y = f|\theta) = \frac{e^{\sigma_d \alpha_{if}}}{\sum_{f=1}^{F} e^{\sigma_d \alpha_{if}}}$$

where $a_{if}$ is the attraction score towards food type *f* of individual *i*, and $\sigma_d$the selectivity during decision making. The selectivity is a scale that determines how

likely individuals are to pay attention to differences in attraction in the food types. If $\sigma = 0$ then all food types have the same probability of being chosen, whereas if it is very high then individuals are nearly always picking the best choice. The selectivity was set to 1 in all of the following models. I defined $\alpha_{if} = ia_f + \beta Prev_{if}$ where *ia* is the initial attraction to each food type, which can be interpreted as what rewards an individual expects to get from that food type. It is fixed across all events, and across each individual. The priors for these parameters are drawn from a normal distribution N (0,100), because I estimated that the strength of the attraction for each food type can vary widely. *f* is the food type and can range from one to seven: 1 = apple, 2 = grape, 3 = pear, 4 = cricket, 5 = mealworm and 6 = papaya. In order to fit the values for the initial attraction in the model, the initial attraction for the familiar food (banana) was set to zero as an 'anchor' to which the other food type associations could be compared, since all individuals should be familiar with this food type. The fitted parameters are therefore the association for apple, grape, pear, cricket, mealworm, and papaya, so that those initial attraction values predict the likelihood of choosing those food items. *Prev* are the parameters fitted based on the data of the first phase based on previous experience: (1) eating events, (2) explore events, (3) unsuccessful food transfers (UFT), (4) scrounging, (5) successful food transfers (SFT) and (6) observation events. One $\beta$ is fitted for each parameter corresponding to each previous experience. The parameters are unknown and random, and so are also drawn from a normal distribution N(0,100) (van de Schoot et al., 2014). On top of obtaining parameter estimates, I also calculated their 95% credible intervals, which are the Bayesian perspective on confidence intervals (Nakagawa & Cuthill, 2007).

Markov Chain Monte Carlo (MCMC) was used to derive a posterior sample for each parameter, which can be used to approximate the posterior distributions and thus make inferences about those parameters. Each data point in the MCMC chain is a parameter sample (i.e. one instantiation of drawing all the parameters from the posteriors). Four MCMC chains were run to ensure that chains were converging and mixing well. A thinning of five was also used to prevent autocorrelation. This process was repeated to give sample of 5000 from each

chain. The model was then run over all the (experimental) data for each sample. To compare models and account for over fitting I used the Widely Applicable Information Criterion (WAIC) (Watanabe, 2013). The WAIC uses the Bayesian posterior distribution to assess a model's fit. WAIC also calculates an effective number of parameters to penalise models that have uneven (high variance) fit across different data points which can be evidence for overfitting (Whalen & Hoppitt, 2016). This is important because as the number of parameters increases, the more likely the model is going to fit the data. But this creates an overfitting problem where the model fits the particular data set very well, but would not fit another data set because it is not general enough: it has been fitted to the specific features of the data set at hand. To adjust for overfitting, WAIC does not use the actual number of parameters in the model, but the effective number of parameters. This is calculated based on the posterior distribution of variance of each parameter: WAIC used the uncertainty of the posterior distributions of each parameter to calculate the "importance" of the parameters in the model. It then penalised the models for the number of "important" parameters in each, and with this information it then computed the WAIC of each model (Watanabe, 2013). Moreover, because I used the models in a predictive context (predicting the food choice of an individual), WAIC has the advantage over AIC of averaging over the posterior distribution rather than conditioning on a point estimate such as the mean or median of the posterior distribution (Gelman, Hwang, & Vehtari, 2014). The WAIC is therefore a criterion that allows us to select how confident we are in the different models.

## 4.2 Chapter 6: Role of food-offering calls in wild golden lion tamarins: evidence for teaching behaviour?

In this chapter I wanted to compare the foraging behaviour of juveniles on a novel substrate between those that received food calls played back, and those that did not. Because of the design, where there was a control and an experimental condition, most of the data analysis resulted in comparing conditions. Hence a two-tailed t-test statistic was used**.** When deciding on the statistical analysis, initially, t-tests were considered to compare conditions.

However, in some cases the assumption of normality was rejected (Shapiro-test; $p < 0.05$), and in cases where it was not, this may simply have been the result of low power to detect departures from normality with a small sample size. Therefore, Mann-Whitney tests were then considered next, finding a similar pattern of significance, but with higher p-values. However, higher p-values are likely to be a result of the lower power of this test. Consequently, I present the results from a randomisation test in which the two-tailed t-test statistic was used, but the null distribution was generated by randomising the data between the conditions 100,000 times. Such randomisation tests make no assumptions about the distribution of the data, and have similar power to parametric tests (Manly, 2006). Results with $p<0.01$ or $0.01<p<0.05$ are taken to be strong or reasonable evidence of a difference respectively; results with $0.05<p<0.1$ are taken to be suggestive of a difference due to an unavoidably small sample size (four juveniles in the experimental condition and three in the control) (see 6.5.2.1).

Moreover, because null hypothesis testing does not provide the magnitude of the effect that is of interest and the precision of that effect, I also provided effect size statistics and their confidence intervals (CIs) calculated with Nakagawa and Cuthill's (2007) method. This enables a more efficient assessment of the relationships in the data, regardless of their statistical significance since the effect size measures the strength of a relationship, while the confidence intervals show the precision of an estimation (Nakagawa & Cuthill, 2007). Following Field et al. (2012), effect sizes are reported as large when they explain at least 25% of the variance in the dependent variable ($r > 0.5$). The effect sizes are also very useful for future potential comparison with independent studies (Nakagawa & Cuthill, 2007).

## 4.3 Chapter 7: A follow up on Nicol and Pope's (1996) study: evidence for teaching behaviour in domestic fowl?

In this chapter, the aim was to replicate Nicol and Pope's (1996) findings, and further evaluate whether the young would learn which food to peck from observing the hen. Hence, unlike in Chapter 5, no Bayesian or information-theoretic approach was used. Instead, I used a frequentist approach in order to make the results more easily comparable to Nicol and Pope's (1996) findings. However, unlike Nicol and Pope's (1996) experiment, both hens and chicks in my experiment did not peck only at the colour they were trained on. Hence, because each hen and chick pecked at a varying proportion of red food, I used mixed-models rather than a within-individual paired comparison (as was used in the original experiment).

Where appropriate, I tested for normality and checked the homogeneity of variance for all models, by plotting the residuals against the fitted values. When the variance was not approximately homogenous, I used the generalized least squares (GLS) method, using the *nlme* package (Pinheiro, Bates, DebRoy, Sarkar, & R Development Core Team, 2016), which deals with heteroscedasticity. This method adds a weight to the predictor variable and allows for a larger residual spread if the variable increases in cases of continuous variables, or allows the variance to differ for each category for nominal variables. When the continuous variable included a value of zero (when some individuals did not perform that behaviour during that time period), I used the exponential variance structure, which models the variance of the residuals as the variance ($\sigma^2$) multiplied by an exponential function of the variance covariate and an unknown parameter $\delta$, following this structure: $var(\varepsilon_{ij})=\sigma^2 * e^{2\delta x covariate_i}$, where *i* is the number of observations and *j* is the number of categories in the independent variable (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Because all models included random effects, I fitted models with the *lme* function of this same package (Pinheiro et al., 2016). It allows models to be fitted in a similar manner to GLS models, but also allows for one random effect. To know which, if any, variable was important in causing heteroscedasticity I constructed models that included no weight for any

variables, and models that included a weight for each variable one at a time. I chose the model with the lowest AICc score to make inferences. In the majority of best fitting models, the variance was not weighted by any variables, but I report when this is not the case.

In cases where response variables were proportions that sometimes took the value zero or one, I used an empirical logit transformation, meaning I added the minimum non-zero proportion to both the numerator and denominator of the logit function (Warton & Hui, 2011). This introduces a minimal bias, and according to Warton and Hui (2011) this is preferable to an arcsine transformation.

Effect sizes for the anova were calculated with the *mes* function of the *compute.es* package (Del Re, 2013), and are reported as omega ($\omega$) (Field et al., 2012).

# Chapter 5:

# Role of food transfers in wild golden lion tamarins: evidence for teaching behaviour?

## 5.1 Abstract

This chapter examines whether the role of food transfers in wild golden lion tamarins (GLTs) is to teach juveniles which foods are good to eat. To study this behaviour I introduced different types of food (familiar, novel, fruits, insects) and monitored rates and types of food transfers between adults and juveniles. First I analysed which types of foods are preferentially transferred from adults to juveniles and then investigated whether adults or juveniles direct the transfer decisions. Next I used Bayesian statistics to model the juveniles' foraging choices five months after the introduction of the different food types based on their previous experience with those food types. I paid particular attention to the role of prior food transfer experience. I found little evidence that novel foods are transferred more than familiar ones. This pattern of transfer is not driven by juveniles attempting to obtain more novel foods, or by adults attempting to discard more novel food, compared to familiar ones. Moreover, food transfers seemingly play a role in the juvenile's foraging decisions. This suggests that despite the lack of teaching, juveniles still learn from food transfers.

## 5.2 Introduction

### 5.2.1 Parental care

Parental care is the investment of parents towards the development and survival of their offspring. It occurs in multiple lineages and given its phylogenetic distribution, parental care unsurprisingly can take very different forms of behaviour ranging from the construction of nest and burrows, production of resources for eggs, care of eggs and/or young within and outside the parent's body (nourishing, incubating, defending, transporting) (Danchin, Giraldeau, & Cezilly, 2008). In some species parental care is mainly maternal (mammals, birds) while in others paternal care is more important (fish). Biparental care and alloparental care also happen in some taxa but remain quite rare. Alloparental care mainly occurs in cooperatively breeding species, where group members other than the parents invest in survival of the young. Like parental care, alloparental care can also take a variety of forms and even lead to

the extremely costly case of lactation in non-breeding females that has been found in meerkats (Creel, Monfort, Wildt, & Waser, 1991).

The benefits of parental care to adults are quite straightforward: to increase the survival rate of the offspring, hence increasing the parent's reproductive fitness. However the costs are harder to evaluate as they can be both immediate (e.g. loss of resources, increased predation risk) and delayed (e.g. lack of investment in future offspring) (Nordell & Valone, 2015). Parental care can also have both short and long term repercussions for the offspring's survival. Offspring can immediately benefit from parental care by getting resources that they would not have acquired otherwise or gaining protection from predators. But offspring can also benefit on a longer time scale. For instance juveniles can acquire information about their environment, acquire skills, or acquire strategies to obtain that information and those skills, through parental care. One of the better known long-term impacts of parental care is shown in Weaver et al.'s (2004) study of the licking and grooming behaviour of mother rats which influences the pups' long-term stress response, and in a later study the pups' reliance on social learning (Lindeyer et al., 2013). But as Brown et al.'s (2004) review of food transfers in nonhuman primates highlights, short and long term impacts of parental care on the development of juveniles are not mutually exclusive.

### 5.2.2 Alloparental care and food transfers

GLTs are a cooperatively breeding species, which means that every member in the group contributes to raising the young. This is an adaptive strategy, as alloparental behaviour seems to increase the reproductive success of the breeder. In fact, Mitani and Watts (1997) found, with a comparative analysis, that in primates, allocaretaking correlates with relatively fast infant growth and reproduction. There are also correlational data in callitrichids showing a relationship between allocaretaking and rapid infant growth and reproduction (Goldizen, 1987; Ross, 1991). Moreover, the number of helpers in the groups is found to be positively correlated with infant survival in some populations of lion

tamarins (Bales et al., 2000) but not in others (Baker et al., 1993; Dietz & Baker, 1993).

Food provisioning is one example of parental care. In primates, although infants spend a lot of their time feeding with their group members, direct food transfer is quite uncommon in old world monkeys. Although it is prevalent in apes (except in gorillas), it is mostly infant initiated (see Rapaport & Brown, 2008). Callitrichidae is a New World primate family that is unique not only in terms of the extent of food transfers to infants, but also for the prevalence of active giving where the transfers are initiated by the adults (G. R. Brown et al., 2004; Feistner & McGrew, 1989). In primates, most food transfers occur between mother and infants (Feistner & McGrew, 1989) but since GLTs are cooperative breeders, every member of a group contributes to this behaviour.

It has been established that the presence of alloparents in primate species, including tamarins, does appear to correlate with increased infant survival rate, in some cases. However the precise role of food transfer by all group members in infants' growth and development is still relatively unknown.

### 5.2.3 Golden lion tamarins and food transfers: Hypotheses and predictions

In GLTs, food transfers are frequent and can happen between all group members, but are particularly prevalent towards immature individuals and sometimes towards pregnant females (Ruiz-Miranda et al., 1999). Adult-adult food transfers in primates can usually be explained by trade and reciprocity (Nishida, Hasegawa, Hayaki, Takahata, & Uehara, 1992; Teleki, 1973), where more egalitarian societies with shallow dominance hierarchy engage in more transfers (Jaeggi, Stevens, & Van Schaik, 2010), or can be the least costly option compared to potential harassment (Stevens, 2004). However the experiment in this chapter focuses on the role of food transfers in the development of the juveniles, where it is unlikely that these factors play an important role in explaining food transfer behaviour (G. R. Brown et al., 2004). In GLTs, adult-

juvenile food transfers seem particularly important for the development and survival of the young as juveniles are dependent on others to receive their first solid foods, and initially typically receive most of their solid food from food transfers. A captive study found that GLTs still receive up to 90% of their solid food from others at 16 weeks of age (Hoage, 1982), before gradually becoming independent foragers by nine months of age.

Adult-juvenile food transfers can have short-term benefits for the recipient as they allow the offspring to receive nutrients and energy that it might not have had otherwise. This is the *nutritional* hypothesis of food provisioning. But food provisioning can also have longer-term benefits. For instance, while transferring food, adults can also transfer information about the food items' quality or processing techniques. The young can then re-use this information as they mature, and increase their survival chances across their lifespan. If information or skills are also transferred, this could help young to reach nutritional independency by allowing them to learn about diet breath and/or foraging skills of the species. This is called the *informational* hypothesis. The hypotheses are not mutually exclusive, as receivers of a food transfer can obtain both nutritional value from that food item, as well as information about its palatability or quality.

### 5.2.4 Evidence of food transfers as teaching in this species

In the wild, food items that are voluntarily transferred to juvenile GLTs are more likely to be vertebrate and invertebrate prey (which constituted up to 51% of the transferred items in Ruiz-Miranda et al., 1999), than fruits. In a captive study with lion tamarins, Price and Feistner (1993) found that when food items are more difficult to acquire for juveniles (out of reach), and when items are presented singly (rare) rather than all at once, food transfers from adults to young increase and so did the adult's response to juvenile begging. The results from this captive study suggest that food transfers in lion tamarins allow juveniles to receive adequate amounts of food. However, another study on captive GLTs by Rapaport (1999) found that novel foods (be they novel to all

individuals or novel to the young but familiar to the adult) are transferred to juveniles more than familiar ones. This would support the *informational* hypothesis. Price and Feistner (1993) however found that although juveniles ate less of the novel food, this pattern was not compensated by an increased transfer of those foods from adults to juveniles. This second result suggests that food transfers are not used to transmit information to juveniles about what to include in their diets. However, it should be noted that in this study only one golden lion tamarin took part in the experiment, the other subjects being golden-headed lion tamarins and black lion tamarins. Moura et al. (2010) found that in captive golden-headed lion tamarins transfers occurred more often when the food was difficult to access than when it was not, but also found that when novel food was available, transfers decreased compared to familiar food (Moura & Langguth, 1999). They suggest that this later pattern was due to an avoidance of potentially toxic food, and that juveniles might learn what to eat or what not to eat this way.

The seemingly contradictory results between Rapaport (1999) and Price and Feistner (1993) could highlight the dual role of food transfers in GLTs depending on the juveniles' age. In fact, in Price and Feistner's (1993) study the juveniles were younger (7-21 weeks) than in Rapaport's (1999) study (13-37 weeks). Consequently young juveniles, who sustain a high growth rate, might primarily receive food that they would not be able to acquire otherwise (*nutritional* hypothesis), while older immature individuals might mainly receive food that they have not sampled yet. Therefore food transfers to older juveniles might be used to inform them about what foods to select (*informational* hypothesis).

The *informational* hypothesis can also be linked to teaching behaviour in this species. In fact, for a behaviour to be considered teaching, an individual needs to 1) modify its behaviour in the presence of a naïve observer, 2) this modification needs to come at a cost or at least no direct benefit, and 3) the naïve observer needs to learn a skill or information either earlier in life or that it would not have otherwise (Caro & Hauser, 1992).

In some callitrichids, juveniles beg more for novel food then they do for familiar items (G. R. Brown, Almond, & Bates, 2005; Voelkl, Schrauf, & Huber, 2006). If, as a consequence of their begging behaviour, juveniles would receive more novel food than familiar food then they would be the ones responsible for this pattern of transfers (Feistner & Price, 2000; E. C. Price & Feistner, 2001). However, both Rapaport (1999) and Price and Feistner (1993) found that juveniles beg as much for novel as for familiar food. Thus if juvenile GLTs obtain more novel food than familiar food, as Rapaport's (1999) results suggest, the adults (donors) would be responsible for that pattern, and not the juveniles (receivers). This would therefore fulfil the first criteria of Caro and Hauser's (1992) definition. There is suggestive evidence that food transfers in GLTs could be a form of teaching behaviour, but this remains to be seen in the wild. Moreover, the key difference between the *nutritional* and *informational* (and hence teaching) hypothesis is whether food transfers result in infant learning. This has never been directly tested previously, and it is an aspect on which I am focusing in this chapter.

### 5.2.5 Aim of the experiment

According to work done in captivity on GLTs, juveniles beg indiscriminately for familiar and novel food, but adults relinquish more novel food than familiar food to the young (Rapaport, 1999). Therefore, the first aim was to see if Rapaport's (1999) findings hold in the wild, i.e. whether adults modify their food transfer behaviour in presence of juveniles. The interest was in the decision of a potential food donor to transfer different food items. Juveniles were at least 17 weeks old at the start of our study, so that findings could be comparable to Rapaport's (1999). If food transfers were mainly for *nutritional* purposes, we would expect that the food novelty has no impact on the pattern of transfers: either all food items are transferred equally, or the most nutritious food are preferentially transferred. If transfers serve mainly for an *informational* objective, then we would expect novel, rare or difficult to process food items to be transferred to a greater extent. Consequently, novel food items should be preferentially transferred over familiar items solely in the case of the

*informational* hypothesis. Moreover, if those transfers play a role in transmitting *information* from a knowledgeable individual to a naïve one, it is expected that the naïve individual would learn about the properties of the food items being transferred, and hence develop foraging preferences from those social interactions. A third hypothesis can also explain the food transfer behaviour between adults-juveniles in GLTs. This is the *harassment-avoidance* hypothesis, where adults transfer food to juveniles because it is the least-costly behavioural option for them. In this case, it would be expected for all food types to be transferred equally, similar to the *nutritional hypothesis*, but also for juveniles to be the drivers behind food transfer patterns. It might also be expected that in this case the least valuable food are preferentially transferred.

Even if Rapaport's (1999) findings were reproduced in the wild, it is still unknown whether the food transfer behaviour fulfils the third criterion of Caro and Hauser's (1992) definition: do naïve individuals learn from the modified behaviour? Thus, I also wanted to examine the potential learning resulting from food transfers and other social components of GLTs' foraging behaviour. To look at the potential long-term effects of those food transfers I conducted an experiment over several months to look at the impact of transfers on juveniles' foraging preferences after the juveniles had reached foraging independence.

The experiment has two goals:

1. **To establish whether wild adults do actively transfer novel food more readily then familiar food, to juveniles, as found in captivity (Rapaport, 1999).** This is examined when they are still highly dependent on adults for food acquisition (first phase)**.** Allied to this objective, I also want to determine:
    - **1.1 Whether the juveniles are the drivers behind the food transfer patterns observed by investigating the probability of a juveniles attempting a transfer and the probability of succeeding in obtaining food given that the adult is resisting the transfer.**

1.2 **Whether the adults transfer novel food types in order to terminate harassment by juveniles by investigating the probability of an adult resisting the transfer, and therefore the likelihood of adults keeping the food for themselves.**

2. **To establish whether the food choices of independently foraging juveniles (at 10-11 months of age – second phase) are related to the amount of food transfer received when they were four to six months old.**

In this chapter, I will first cover the methods, both experimental and statistical before explaining the results of the first phase of the experiment which looked at the nature of the transfers, and the second phase of the experiment, which looked at the juveniles' learning. I will finish by discussing the implications of food transfers on the development of the young, and its relation to teaching behaviour.

## 5.3 Methods

### 5.3.1 Subjects

Seven groups of wild GLTs from the Poço das Antas and Imbau region were initially studied. All individuals within each group were related to the breeding pair, except in three groups where one individual was not. At the start of the experiment all juveniles were between 17 and 22.5 weeks old. Group POR2 was unreachable for part of this experiment and as a consequence was left out of the analysis. Before the start of the second phase, group AF2 had lost both juveniles. Thus although the experiment included group AF2 and the analysis of the first phase includes both juveniles, the analysis of the second phase does not. The group Alone also lost one of its juveniles between the first and second phase of the experiment. Hence, both juveniles are included in the analysis of the first phase, but only one is included in the analysis of the second phase. For the analysis of the first phase there were N = 10 juveniles, while for the analysis of the second phase there were N = 7 juveniles (N = 44 individuals in total in the six

groups of the first phase and N= 31 individuals in total in the five groups of the second phase) (see Table 2.2 for the list of individuals).

### 5.3.2 Apparatus

Limited amounts of each food were presented in separate, clear, plastic pots that were attached to a platform or to branches at human chest level (Fig. 5.1). The pots were approximately 7 cm in diameter and, 5.5 cm in depth. All members of the group could be on the platform at the same time, but the size of the pots limited the access to approximately four individuals on each pots at the same time.

Figure 5.1: Trial during the second phase of the experiment with group AF2

### 5.3.3 Procedure

As in the food-offering call experiment in Chapter 6, this experiment took place over two time periods: the first phase provided the opportunity for adults to transfer food to juveniles, and the second phase allowed me to assess the juveniles' foraging decisions when they were independent foragers.

#### 5.3.3.1 First phase

The first phase of the experiment took place between January and March 2014. In the first phase, each group was exposed to five food options at the same time. These were: apple, banana, cricket, grape and mealworm (see Table 5.1). Food options were arranged semi-randomly to ensure that most of the time the insect types were not adjacent to each other, and that when the trial did not occur on a platform (where the pots could be arranged in a circle) the familiar food had a fairly central place. Both insects and fruits were used for the novel food to replicate the GLTs' natural diet. Banana was a familiar food for all GLTs (see 2.6.2), while the other fruit options were novel. The fruits were considered of lower nutritious value than the insects (see Table 5.1). Insects were dehydrated and from a local supplier (Nutrinsectat). Crickets were used because they are part of the GLTs' diet in the wild, and were considered to be familiar prior to the experiment, and highly nutritious. Hence, the design was to have two familiar food options, one of lower nutritional value (banana) and one of higher nutritional value (cricket), and three novel food options, two of lower nutritional value (apples and grapes), and one of higher nutritional value (mealworms). Two different fruits were used as novel options to account for differences in texture, and potentially in preferences. This design would have allowed to tease apart whether GLTs transfer more readily highly nutritious food, or more readily novel food, or a combination of both. However, because the wild GLTs in the experiment did not readily feed on the dehydrated insects, I reclassified the crickets as novel for the analysis. Although this left only one familiar food, there still was variety in the nutritional values and textures of the novel foods. The novel foods were chosen based on the food used in captive studies with callitrichids (G. R. Brown et al., 2005; Rapaport, 1998, 1999; Vitale & Queyras, 1997; Voelkl et al., 2006). The fruits were cut into small pieces (<2cm), to fill the pots, and insects were small enough so that several insects could fill the pots. Individuals had no access to those novel foods outside of the experimental context.

Because individuals were tested in groups, and because I did not have access to the GLTs prior to the experiment, it was not possible to examine individual preferences prior to the first phase. Because GLTs were tested in groups, it was also not possible to know whether the only actors affecting a food transfer were the donor and the recipient, but in the analysis I assumed that they were at least the major actors.

Similar to the food-offering call experiment in Chapter 6, the food items were presented to the subjects over five trials. Trials were not considered valid if there was no interaction with the food, if two or fewer individuals were present on the platform (except for the group Alone in the second phase, where the group size was three), if individuals were present for less than 80 seconds in total, and if the group taking part in the trial was displaced or was displacing another group (see Table 5.A.1 in the Appendix for a list of valid trials). Trials were repeated until five valid trials had been completed per group, and all trials were filmed for later analysis.

#### 5.3.3.2 Second phase

The second phase of the experiment took place between August and September 2014. For the second phase, five trials were conducted for each group deploying the same criteria as in the first phase (Table 5.A.2 in the Appendix). This time, two new novel foods were added to the experiment (papaya and pear) bringing the total food options to seven. The nutritional values of the food options used are reported in Table 5.1. Whereas in the first phase banana was used as a familiar food, and apple, cricket, grape and mealworm as novel food, in the second phase banana was used as familiar food, and apple, cricket, grape and mealworm as prior-adult-sampled food (PAS, according to Rapaport's, 1999, terminology), and papaya and pear as novel food. By the time of the second phase, juveniles no longer relied on food transfers. Moreover, four new juveniles were born between the start of the first phase and the second phase. I added two food options in the second phase to look at the effect of individual experience, and the effect of prior-sampled food on the new juveniles.

Table 5.1: Nutritional values of the food options. – denotes that no information was found

| Food option (per 100g) | Calories | Fat (g) | Carbohydrates (g) | Proteins (g) |
|---|---|---|---|---|
| Apple | 52 | 0.2 | 13.8 | 0.3 |
| Banana | 89 | 0.3 | 22.8 | 1.1 |
| Cricket | 120 | 5.5 | 5.1 | 12.9 |
| Grape | 67 | 0.4 | 17.2 | 0.6 |
| Mealworm | 206 | 13 | - | - |
| Papaya | 39 | 0.1 | 9.8 | 0.6 |
| Pear | 58 | 0.1 | 15.5 | 0.4 |

### 5.3.4 Video analysis

As for all the experiments in this thesis, videos were watched using the software package VLC. Behaviours were recorded on Microsoft Excel using the definitions given in Table 5.2. The time and duration of those events were logged, and additional individuals with whom they interacted (in case of food transfers) were also noted. During data extraction the behaviours were recorded as states, but treated in the analysis as events. 10% of the data were double coded and the inter-observer reliability was found to be high ($r=0.95$, $p<2.2e-16$).

Table 5.2: Definitions of the dependent variables

| Behaviour | Definition |
|---|---|
| Exploring | The individual shows interest in the food by orientating its face towards the food and being close enough to sniff it (no physical contact, but close proximity) or handle the food (physical contact) without putting the items in its mouth. |
| Eating | Ingestion of food obtained from the pots. |
| Scrounging | Ingestion of food obtained from outside the pots (platform, branch or ground). |
| Food transfer | Events where an individual actively transferred food were really rare in the data. Hence, I define food transfers as any interaction between two individuals involving a food item. This includes an individual offering the food item it has to another individual, but also events were one individual attempts to obtain a food item from another individual, either by emitting vocalisations or by reaching out an arm in that direction. A successful food transfer is a food transfer in which the receiver obtained some food from the donor. |
| Eating transferred food | Ingestion event that resulted from a successful food transfer. |
| Observation | Observation events were calculated in the following way: once an individual had arrived on camera, it was assumed that it would observe every event of every other individual that was also on camera. This was calculated for all ingestion events: eating, scrounging and social eating. |

For food transfers, the identity of both receiver and donor individuals was recorded, as well as whether the receiver emitted any vocalisations or stole food (the receiver obtains food despite the donor resisting at the time where the receiver obtains the food item). Whether the donor resisted the transfer was further recorded (turns away from the receiver, holds on to the item while the receiver is trying to get it, or runs away), and so was whether it gave up the food item (the donor lets the receiver take the food) or offered it to the receiver (the donor actively, through vocalisation or gesture, invites the receiver to come get the food item). If the donor was resisting at the time when the receiver obtains the food item, it would be classified as the item being stolen. Finally whether or not the transfer was successful (the receiver obtains part or the entire food item – this does not necessarily lead to eating transferred food as on some, very rare, occasions, the receiver obtained food from the donor, but then dropped or discarded it before ingesting it) was also noted. Unsuccessful food transfer occurred when a food transfer was attempted but the food did not change hands. There is a wide range of food transfer types that have been recognised in callitrichids, from a donor actively sharing food, passively sharing it, food being eaten out of the hand of the donor or food being stolen (Feistner & Price, 1990; Hoage, 1982; Rapaport, 1998). Previous studies have also distinguished different types of food transfers, but analysed them together. Because of the rarity of food transfers where the donor actively transferred food to the receiver, I first describe findings with those voluntary transfers before statistically analysing all types of food transfers, and looking at more subtle behavioural cues such as juveniles' attempts and adults' resistance to transfers. In fact, in Rapaport (1998) passive sharing and resistance during food transfers are used to represent the willingness or lack of willingness to surrender a food item. I also use the presence of resistance to understand donors' willingness to transfer food.

For each ingestion event (eating, scrounging, and eating transferred food), I also noted what happened at the end of the ingestion: whether the food item was consumed entirely (finished), dropped or taken by another individual.

### 5.3.5 Teaching model explanation

In order to establish whether food transfers in golden lion tamarins qualify as teaching, I assess whether the behaviour meets Caro and Hauser's (1992) three criteria. To this end I break the statistical analysis of the data down into a number of statistical models to assess each of the criteria. I first explain how these models relate to Caro and Hauser's (1992) criteria before specifying the models in detail in the following section (5.3.6).

#### 5.3.5.1 First criterion: Modified behaviour

The first criterion of Caro and Hauser's (1992) definition is that the demonstrator A (in our case, adult or subadult golden lion tamarins) modifies its behaviour in presence of a naïve observer B (~ four month old juveniles). Furthermore, as argued above, food transfers need to be modified in a way that specifically promote learning, over and above the form the behaviour would have if it had evolved purely for a provisioning function.

If the function of food transfers is to promote learning rather than to purely provide nourishment to the young, I would expect adults to transfer novel food to the juveniles more readily, compared to familiar foods. I predict this would be the case, as it would promote learning of a larger diet. To test this, I defined an attempted food transfer to be any case where a juvenile attempted to obtain food from an adult (who may or may not have emitted a food call in the direction of a juvenile), by begging or by reaching out to take the food. If food transfers have a teaching function, it would be expected that the probability of success of an attempted food transfer involving a novel food would be higher than the probability of success for familiar foods, thereupon giving the juvenile the opportunity to learn. Food transfers included transfer where the donor was resisting, and or when the item was stolen, but I later tested for patterns in resistance during food transfers. Hence I modelled the probability of success of an attempted food transfer, and looked at several variables that could affect it. I was first and foremost interested in whether the type of food (novel or familiar)

would impact the probability of success, and thus looked at the effect of *food familiarity* as a binary variable [the item was a banana (familiar), or was not]. I was also interested in whether individuals updated their knowledge on the food types during the course of the experiment. Accordingly I included an *option specific success* (OSS) variable for both the *receiver* and *donor* individuals, where 'option' refers to the different food options available to the GLTs. OSS calculates the number of each food item previously ingested at any given time for any given individual. This variable was included to test whether there was a possible familiarisation with the food items as the experiment went on. I also included variables giving characteristics of individual receivers and donors such as *age* (discrete variable: infant, juvenile, subadult, adult) and *sex* (binary).

Although I was interested to see if food transfer events were more likely to be successful if the transferred item was novel, this could be due to factors other than teaching. For instance, an increased probability of success in a food transfer for novel food could also arise if juveniles are more highly motivated to get novel food compared to familiar food. Therefore, this alternative hypothesis needed to be assessed.

There are two ways to measure the recipients' motivation to obtain novel food compared to familiar food. First, I examined whether juveniles attempted to obtain more novel food than familiar food. In fact, in other tamarin and marmoset species, juveniles do attempt to obtain more novel compared to familiar food, which means that if any information is transferred along with the food, it is at least partly due to the juveniles' actions, as opposed to the adults' (G. R. Brown et al., 2005; Feistner & Price, 2000; Voelkl et al., 2006). However, in captive golden lion tamarins, it was found that juveniles beg indiscriminately for novel and familiar food, supporting the fact that if any information is transferred, it is due to the adult's behaviour not the juvenile's (Rapaport, 1999). I wanted to find out if this was also the case in wild golden lion tamarins and I looked at what variables could affect the probability of begging for different types of food.

A second way to assess whether juveniles are more motivated to obtain novel food is to focus on cases in which the adult resists giving up food to a juvenile that is attempting to take it. I investigated whether juveniles were more likely to succeed in getting food for novel compared to familiar food, given that there was such resistance in a transfer. I therefore modelled the probability of success of a transfer, given the presence of resistance in that transfer, including the predictor variables described above.

It is conceivable that food novelty might operate simultaneously on both the donor (supporting a teaching function for food transfers) and the motivation of potential recipient. Consequently, I additionally directly examined the effect of food novelty on the donor's actions during an attempted food transfer. In fact, if adults prefer familiar food, they might be more likely to resist a transfer of familiar food when a juvenile is attempting to obtain it than a transfer of novel food. So although we would observe a pattern suggestive of adult actively modifying their behaviour (increased success in food transfers for novel food) it could be explained by mechanisms other than teaching such as the adult's lesser attraction to novel food and their increased probability of giving away those food items. I used resistance to measure whether adults really give up novel foods more easily compared to familiar food in order to identify the adult's motivations behind the food transfer patterns. I modelled the probability of resistance in attempted food transfers, and was primarily interested to see if food familiarity had an effect.

In the second part of the experiment, adults had experience with the previously novel foods, but not with two new novel foods that were added (papaya and pear). Moreover, four individuals (in two groups) that were born in February 2014 had now reached the stage of juveniles: they were approximately 7 months old at the start of the second phase. Those juveniles would have found all of the food types novel except for bananas, but all the other individuals would have had experience with all of the foods except papayas and pears. We therefore had bananas as a familiar food, apples, cricket, grapes and mealworms as prior-adult sampled food and papayas and pears as novel food. According to

Rapaport (1999) we would expect prior-adult sampled food to be transferred with more success than both familiar and novel food, if transfers were used for teaching purposes, because those are food options that are novel to the juveniles but about which the adults are knowledgeable. I therefore ran an analysis on the probability of success of a food transfer based on the data of the second phase of the experiment.

#### 5.3.5.2 Second criterion: Cost

The second criterion of Caro and Hauser's (1992) definition states that for a behaviour to be considered teaching it must have a cost, or at least be of no direct benefit to the individual performing the action. Not only does transferring food to juveniles have no direct benefit to the adults, but it also incurs a cost since the adult gives up food it spent time and energy foraging. No analysis is necessary to establish that this is the case.

However, as Hoppitt et al. (2008) note, Caro and Hauser's (1992) cost criterion is only partially successful in differentiating teaching behaviour from behaviour with alternative functions. This is particularly true for provisioning behaviour, a costly behaviour that can lead to naïve individuals learning about food preferences as an evolutionary by-product of parents provisioning the young for immediate nutritional benefits (rather than for a teaching function). Hence, Hoppitt et al. (2008) suggest that for such behaviour to be considered teaching, evidence would be required to show that it has been modified to promote learning, and in our case, that the provisioning behaviour has been modified specifically to promote the acquisition of food preferences. Hence I expect novel food to be transferred more than familiar food, so that juveniles learn to incorporate novel food in their diet.

#### 5.3.5.3 Third criterion: Learning

Caro and Hauser's (1992) third criterion states that the naïve individual needs to learn a new knowledge or skill, or learn it more efficiently or earlier in life than it would have otherwise, as a result of the demonstrator's modified

behaviour. Consequently, the final aspect of teaching behaviour that I wanted to explore in the food transfer context in golden lion tamarins is whether juveniles learn from the adult's modified behaviour or not. In order to assess the third criterion, I used Bayesian models of juvenile foraging strategies, which modelled the juveniles' food choices as a function of their prior social and asocial experience. I used the first trial of the second phase for the data of juveniles' foraging decisions and compiled all the prior experience of juveniles from the first phase into predictors, with a particular interest to see if successful food transfers had an effect.

Several models were compared to understand whether any of the predictors had an effect on the juveniles' choices, whether juveniles' decisions were influenced by asocial (eating, exploring), social experience (scrounging, observation) or potential teaching experience (food transfers).

Based on Rapaport's (1999) findings, it might be expected that juveniles learn what food are good to eat. However, in the wild it is also possible that they learn to associate particular areas or substrates with food, or that they improve their foraging or handling skills, given that transferred items are mainly prey.

### 5.3.6 Statistical analysis

#### 5.3.6.1 Patterns of food transfers: Modified behaviour?

##### *5.3.6.1.1 Probability of succeeding in a food transfer*

I used the binary dependent variable, success/failure in a food transfer, to model the variables affecting the probability of an individual succeeding. Four main explanatory variables were used. The first three variables were dependent on the food option, *F*, involved in a given food transfer. *Food familiarity* is defined as whether *F* was familiar to the tamarins prior to the experiment's start. Before the pilot study the subjects in this experiment had prior interaction with only one of the food types: bananas, which is classified as "familiar food". The subjects had no previous experience with all other food types used in this

experiment, and those are classified as "novel food". *Donor success* was the amount of *F* (number of food items) the donor individual had consumed during the experiment prior to the food transfer in question, whereas *receiver success* was the equivalent variable for the potential receiver. *Donor age* and *receiver age* were binary variables representing whether the donor and potential receiver respectively were a juvenile or not. Finally, *donor sex* and *receiver sex* gave the sex of each individual involved in the food transfer.

I then refit the set of models replacing the continuous variables *donor success* and *receiver success* with corresponding binary variables, indicating whether *donor success >0* and whether *receiver success >0*. This was to allow for the possibility that consuming a single food item of type *F* may be sufficient for the food to become familiar to a tamarin, or that individuals are neophobic and might require at least some experience with the experimental set up before adopting their usual behaviour. Indeed, when exploring the data, there seemed to be a big difference between having had any experience with the food item, and having had none. Similar models were then fitted on data restricted to transfers from non-juveniles to juveniles.

I initially used nested random effects of *receiver* and *donor individual* within *groups*, but the effect of *group* was estimated to be very small (variance = 0) and did not have any significant impact (p=1), so I dropped *group* as a nested random effect from the model to aid convergence of the model optimisation.

Some studies with callitrichids haves found that fathers were more involved in food transfers, compared to other group members. Although we did not know the paternity of each individual, we looked at this eventuality in our dataset by adding an interaction between the age and sex of the donor (adult male).

#### *5.3.6.1.2 Probability of attempting a food transfer*

I then used another binary dependent variable, presence/absence of an attempted food transfer during an ingestion event, to model the variables that could affect the probability of individual juveniles attempting to obtain food from another individual when an opportunity arose to do so. In this model, the data used were restricted to transfers in which potential receivers were juveniles and potential donors were non-juveniles. Because I was only interested in the probability a potential receiver would attempt a food transfer, I only included the *receiver success* as a binary variable, and not the donor success in the independent variables, as well as *food familiarity*, and *donor* and *receiver sex.* For each combination of potential receiver, potential donor, food familiarity and receiver success I calculated the number of opportunities for attempting a food transfer, defined as an event in which a potential donor was ingesting a food item and the potential receiver was present at the time of the event. I then calculated the number of these events in which a food transfer was attempted to obtain the dependent variable for the analysis. Random effects were included as above.

#### *5.3.6.1.3 Probability of resistance (during a transfer)*

To model the effect of the variables on the probability that the donor resisted a transfer, I used the binary dependent variable of presence/absence of resistance in a food transfer. The data were therefore restricted to food transfer events only, and also restricted to juvenile receivers and non-juvenile donors. The presence of resistance in a transfer was modelled as a function of *food familiarity*, previous *success* and *sex* of both the donor and receiver. The analysis was conducted with both of the individuals' previous *success* variables as continuous variables. The analysis was then repeated, with the *success* variables replaced with their binary equivalents as described above.

In both analyses a number of models did not fully converge when including both random effects, despite increasing the number of iterations in the

optimisation algorithm to 1,000,000. To check that this did not influence the results greatly, I reran each analysis three times, once with each of the random effects and again with no random effects. All models (no random effect, *individual receiver* as random effect, *individual donor* as random effect) showed similar results to the initial analysis in that no support for any of the explanatory variables was found. Therefore in the results section (5.4.1.4) I only report the results of the analysis including both random effects.

#### *5.3.6.1.4 Probability of succeeding in a food transfer, given resistance*

Similar to 5.3.6.1.1, in order to model the effect of the explanatory variables on the probability of succeeding in a food transfer, given resistance in the transfer, I used the binary dependent variable, success/failure in a food transfer, but restricted the data to food transfers in which the donor resisted the transfer. The explanatory variables were *food familiarity*, previous *success*, *age* and *sex* for both *receiver* and *donor* in all cases. Four analyses were conducted: two included all the food transfers where there was resistance, with one analysis treating (*receiver* and *donor*) *success* as continuous variables, and the other treating *success* as binary variables (see above). These analyses were then repeated restricted to only non-juvenile to juvenile transfers. I ran the analysis on the two data sets to compare it with the analysis in 5.3.6.1.1, because although I was ultimately interested in the non-juvenile to juvenile transfers, I also wanted to know if there was a more general pattern that would apply to all transfers. In the analyses treating *receiver* and *donor success* as a binary variable, a number of models did not fully converge so the analysis was re-run increasing the optimisation iteration limit to 100,000, which ensured convergence for all models.

#### *5.3.6.1.5 Probability of succeeding in a food transfer in the second phase of the experiment*

To look at the probability of succeeding in a food transfer for the four new juveniles, I ran similar models to the ones 5.3.6.1.1 (on all food transfers and on adult-juvenile transfers) on different data. The data only included the second

phase of the experiment, and therefore seven food types (one familiar, four prior-adult sampled, and two novel). However, because the analysis of the first phase was based on categories of food (familiar vs novel), I wanted to do the same for the second part in order to facilitate a comparison of results. I therefore classified each food type into categories: familiar (banana), novel (papaya and pears) and prior-adult sampled (apple, cricket, grape, mealworm). Because I was interested in the effect of prior-adult sampled foods, I ran the analysis with the novelty variable as a binary: the food was either prior-adult sampled or not (familiar or novel).

Three successful transfers involved an unknown donor, and were all transfers of apples. Those unknown donors were from the group AF2 and were all adults, but I do not know their identity, sex or previous success. I therefore excluded these food transfers from the analysis in order to include the potential effect of *donor sex* and *donor success* >0. All of the four juveniles in the second phase were females; therefore I did not include *receiver sex* as a variable in any of the following analysis. The following models were also all GLMs, because the sample size was too small to include random effects of receivers and donors.

#### 5.3.6.2 Effects of food transfers: Learning?

In order to predict the foraging choices made by juveniles I compared a variety of models; each with different sets of social and non-social parameters, to the data, to find the one that best explains the data. I selected data for the first trial of the second phase for the seven juveniles still alive that were also present in the first phase. I used only the first trial to avoid additional effects of learning. I wanted to predict the individuals' choices in this trial, based on their prior experience with each food type in the first phase, so I summed up the number of behavioural events of the first phase, and used those as predictors. As mentioned earlier, the behaviours used were the number of: (1) eating events, (2) explore events, (3) unsuccessful food transfers (UFT), (4) scrounging, (5) successful food transfers (SFT) and (6) observation events, for each individual for each food type, as defined in Table 5.1 This enabled me to assess which of these events

during the first phase, impacted food choices during the second phase. On top of the parameters that included the prior experience of each individual, there were parameters for the initial association individuals have for each food type. The strengths of those parameters allowed me to determine which food types were preferentially chosen, relative to the familiar food (banana).

I then used WAIC for model comparison, as explained in Chapter 4. Through the model comparison, I aimed to achieve several things. (1) I wanted to test whether successful food transfers have a certain effect on juveniles' food choices. (2) I also wanted to allow for various alternative predictors. (3) I wanted to allow for multiple predictors, because some predictors only work well in combination. (4) I also wanted to control for overfitting by having a minimum number of parameters in the model, especially given the size of the data set. (5) Because testing for all the possible models is not feasible, I developed a strategy to only test a subset of all possible models. Since no one strategy is perfect (or each has downsides), I adopted multiple approaches to obtain more certainty about the patterns emerging in the models. (i) First I adopted a hypothesis testing method where I looked at the effect of particular combination of parameters as well as the effect that successful food transfers might have on the juveniles' choices, as this could be indicative of teaching behaviour. Some issues with this method are that it can overlook various combinations and there are also various different parameter combinations that could in principle fulfil the same hypothesis. The combinations of parameters selected are based on a-priori hypothesis of the possible effects of previous experience on juvenile choice. (ii) I then looked at the full model, and dropped predictors from the model if their 95% credible interval straddled zero, so that their sign could not be attributed with high certainty ("straddle" method). This can however reduce the goodness of fit relative to the best possible model, and is not guaranteed to find the best combination of variables. (iii) The third method adopted was to drop predictors from a full model if this improved the fit (backward stepwise model selection) or add predictors from a baseline model if it improved the fit (forward stepwise model selection) based on the WAIC. This method can also overlook various combinations of dropped parameters that could in principle generate a good fit.

Moreover, this method can be particularly prone to overfitting. (iv) The final method adopted was dropping predictors from the full model if they were highly uncertain (based on the variance of their posterior distribution). Like the other methods, this does not address all possible combinations and thus may not find the best fitting model.

## 5.4 Results

### 5.4.1 First criterion: Modified behaviour

The first criterion is that the demonstrator A (for our purposes, the adults) modifies its behaviour in the presence of a naïve observer B (~4 month old juveniles). I constructed several models to examine if that was the case with my data.

#### 5.4.1.1 Qualitative analysis of food transfers

During the first phase of this study, 233 food transfers were made by 22 adult/subadult (non-juveniles) GLTs and 10 juveniles, split into six family groups. Food transfers comprised 7% of all foraging related behaviour (eating, scrounging and exploring). 111 of the 233 transfers (48%) were successful, meaning the recipient obtained food. There were a total of 1243 successful ingestion events, so GLTs in the first phase of the experiment obtained 9% of ingested food items from food transfers. The potential receiver initiated 95% of the transfers, and 55% of the individual initiating the transfer were juveniles. 70% of the successful food transfers were made with novel food (Table 5.3), and 67% when only juveniles are recipients and non-juveniles are donors (Table 5.4).

Table 5.3: Successful and failed transfer for each type of food

| Transfer | Apple | Banana (Fam) | Cricket | Grape | Mealworm |
|---|---|---|---|---|---|
| Fail | 51 | 44 | 0 | 27 | 0 |
| Success | 38 | 33 | 0 | 40 | 0 |

Table 5.4: Successful and failed transfer for each type of food for juvenile recipients and adult/subadult donors only

| Transfer | Apple | Banana (Fam) | Cricket | Grape | Mealworm |
|---|---|---|---|---|---|
| Fail | 20 | 25 | 0 | 12 | 0 |
| Success | 26 | 21 | 0 | 16 | 0 |

Out of those 233 transfers, only 11 had a donor active and initiating the transfer (5%). All of those donor-initiated transfers were successful, and six of those interactions were transfers of grapes, three were of bananas and two of apples. In all of those transfers the donor was an adult or subadult, but the age of the receivers varied. Seven receivers of donor-initiated transfers were juveniles, while one was an adult and three were subadults. However, all of the non-juvenile receivers were females. Although we do not know if those females were pregnant, this fits with the pattern of previous findings (Ruiz-Miranda et al., 1999). Donors seemed to equally transfer novel and familiar food, however, because all of the donor-initiated transfers were successful, it was not possible to analyse whether the transfers of novel food were more successful than transfers of familiar food. Instead, I ran an analysis over all of the food transfers, and then separately looked at the role of donors through resistance, and the role of receivers through their attempts at obtaining food from other individuals.

#### 5.4.1.2 Probability of succeeding in a food transfer

When investigating the probability of success of all food transfers, the top models fitted are shown in Table 5.5 and results of model averaging are in Table 5.6. *Option specific success* (OSS) was used as a variable to keep track of the number of ingestion events with each food type over time, and how this could affect the individual's knowledge about the food items. There was little support for an effect of *food familiarity* on the probability of success of a food transfer (effect size = -0.11; 95% C.I. = -0.56, 0.34), with the odds of success for an attempted food transfer involving familiar food being 0.89 times lower (95% U.C.I. =0.57, 1.41) than attempted food transfers involving novel food (Fig. 5.2). If the food was familiar, there was an estimated 42% chance of a food transfer being successful, compared to 45% for novel food. There was little support for an effect of the number of *previous option specific* ingestions by the potential *recipient* (effect size = -0.001; 95% C.I. = -0.02, 0.02) or the potential *donor*, as it was not included in any of the top models.

There was some support for an effect of the *age* class of the potential *recipient* as it was the most important predictor (sum of weights = 51%) with the odds of success for juveniles being 1.26 times higher (95% U.C.I. = 0.69, 2.31) than for non-juveniles (adults and subadults), and there was an estimated 51% chance of success in a food transfer for a juvenile compared to 45% for non-juveniles (adults and subadults). How the support for this variable is quite weak as the 95% C.I. for the estimate includes zero. There was also little evidence of an effect of the *age* of the potential *donor* (effect size = -0.20; 95% C.I. = -0.96, 0.56), or of the *sex* of the potential *recipient* (effect size = -0.03; 95% C.I. = -0.28, 0.22) or *donor* (not present in the top models).

Table 5.5: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (continuous) on the probability of success of food transfers (from 233 observations, of 32 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Receiver Age | 4 | 327.04 | 0.00 | 0.14 |
| Null | 3 | 327.35 | 0.31 | 0.12 |
| Donor Age | 4 | 327.53 | 0.49 | 0.11 |
| Food Familiarity + Receiver Age | 5 | 327.83 | 0.79 | 0.10 |
| Donor Age+ Receiver Age | 5 | 328.01 | 0.97 | 0.09 |
| Food Familiarity + Donor Age | 5 | 328.24 | 1.21 | 0.08 |
| Food Familiarity | 4 | 328.38 | 1.34 | 0.07 |
| Receiver Sex + Receiver Age | 5 | 328.58 | 1.54 | 0.07 |
| Food Familiarity + Donor Age + Receiver Age | 6 | 328.58 | 1.54 | 0.07 |
| Receiver Age4+ Receiver Success | 5 | 328.91 | 1.87 | 0.06 |
| Receiver Sex | 4 | 328.91 | 1.87 | 0.06 |
| Receiver Success | 4 | 329.03 | 1.99 | 0.05 |

Table 5.6: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of a success of food transfers

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -0.20 (± 0.28) | -0.75, 0.35 | 0.82 baseline odds of success | 0.47, 1.42 |
| Receiver Age | 0.51 | 0.23 (± 0.31) | -0.38, 0.84 | 1.26x (juveniles/ non-juveniles) | 0.69, 2.31 |
| Donor Age | 0.34 | -0.20 (± 0.39) | -0.96, 0.56 | 0.82x (juveniles/ non-juveniles) | 0.38, 1.78 |
| Food Familiarity | 0.31 | -0.11 (± 0.23) | -0.56, 0.34 | 0.89x (familiar/ novel) | 0.57, 1.41 |
| Receiver Sex | 0.12 | -0.03 (± 0.13) | -0.28, 0.22 | 0.97x (females/ males) | 0.75, 1.25 |
| Receiver Success | 0.11 | -0.001 (± 0.01) | -0.02, 0.02 | 1.00x per previous success | 0.98, 1.02 |

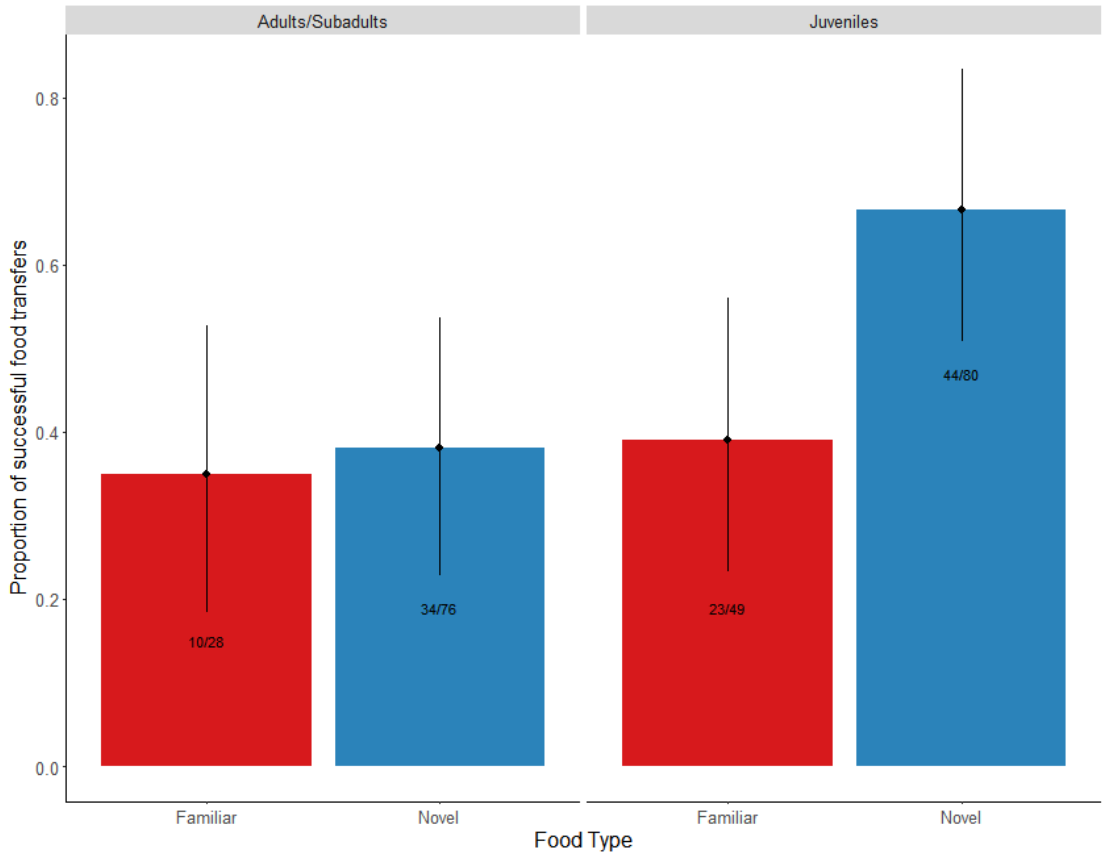


Figure 5.2: Proportion of success of food transfers for novel and familiar food, averaged by individuals, in non-juvenile and juvenile receivers, with standard errors based on the raw data. Error bars are 95% C.I., not assuming normality

Despite the observation of the barplot showing the proportion of success of food transfers for novel and familiar food in non-juveniles and juveniles (Fig. 5.2), there is little evidence for interaction between *food familiarity* and *age* (sum of weights = 7%), hence we present results of model selection without the interaction included, as it helps with convergence. This means that the action of novel and familiar food is the same for juveniles and non-juveniles.

The above results suggest that there is little evidence that food items that were novel before the experiment became less likely to be successfully transferred as the potential donor or recipient ingested more of that food item (i.e. as they became more familiar with it). However, this analysis assumes that the odds of a successful food transfer will be a linear function of the previous number of successes. An alternative possibility is that a single ingestion of a novel food item is enough for a tamarin to become familiar with a food type, and

thus decrease the odds of success, without further ingestion events having an effect.

I therefore tested for an effect of OSS as a binary variable: OSS = 0 versus OSS > 0, to see if tamarins behaved differently before and after having ingested one particular type of food in this experiment. I looked for an effect of this binary variable on both the potential donor (*donor success*) and receiver (*receiver success*) of the transfer. The top models fitted are shown in Table 5.7 and the results of model averaging are in Table 5.8. *Donor success* > 0 (effect size = 1.92; 95% C.I. = 0.92, 2.92) came out as an important variable in predicting the success of a transfer, however there was still little evidence of an effect of *food familiarity* (effect size = -0.19; 95% C.I. = -0.78, 0.40; Table 5.8). Similar to the previous analysis, the odds of success for an attempted food transfer involving familiar food were 0.83 times lower (95% U.C.I. = 0.46, 1.49) than attempted food transfers involving novel food. However, the effect of the donor having ingested a food item at least once is in the opposite direction, with the odds of success for an attempted food transfer being 6.82 times higher (95% U.C.I = 2.51, 18.53; Table 5.8) when the donor had ingested a food type at least once than when the donor has never ingested that type of food, suggesting that a single ingestion event is sufficient for a potential donor to treat a food type as familiar. On the other hand, there was little support for an effect of *receiver success* as a binary variable (effect size = -0.43; 95% C.I. = -1.29, 0.43; Table 5.8), which suggests that one exposure to the food item or experimental context does not change the receiver's behaviour.

Table 5.7: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (binary) on the probability of success of food transfers (from 233 observations, of 32 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Donor Age + Donor Success >0 + Receiver Success >0 | 6 | 320.25 | 0.00 | 0.11 |
| Food Familiarity + Donor Age + Donor Success >0 + Receiver Success >0 | 7 | 320.27 | 0.02 | 0.11 |
| Donor Success >0 + Receiver Success >0 | 5 | 320.76 | 0.51 | 0.09 |
| Food Familiarity + Donor Age + Donor Success >0 | 6 | 320.93 | 0.67 | 0.08 |
| Donor Age + Donor Success >0 | 5 | 320.95 | 0.69 | 0.08 |
| Donor Success >0 | 4 | 321.25 | 1.00 | 0.07 |
| Food Familiarity + Donor Success >0 + Receiver Success >0 | 6 | 321.29 | 1.04 | 0.07 |
| Food Familiarity + Donor Success >0 | 5 | 321.72 | 1.47 | 0.05 |
| Food Familiarity + Donor Age + Donor Success >0 + Receiver Sex + Receiver Success >0 | 8 | 321.81 | 1.55 | 0.05 |
| Donor Success >0 + Receiver Age + Receiver Success >0 | 6 | 321.84 | 1.59 | 0.05 |
| Donor Age + Donor Success >0 + Receiver Sex + Receiver Success >0 | 7 | 321.87 | 1.61 | 0.05 |
| Food Familiarity + Donor Age + Donor Success >0 + Receiver Age + Receiver Success >0 | 8 | 321.88 | 1.62 | 0.05 |
| Donor Age + Donor Success >0 + Receiver Age + Receiver Success >0 | 7 | 321.95 | 1.70 | 0.05 |
| Donor Success >0 + Receiver Age | 5 | 322.04 | 1.79 | 0.05 |
| Food Familiarity + Donor Success >0 + Receiver Age + Receiver Success >0 | 7 | 322.17 | 1.91 | 0.04 |

Table 5.8: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of a success of food transfers

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -1.49 (± 0.71) | -2.88, -0.10 | 0.23 baseline odds of success | 0.06, 0.91 |
| **Donor Success >0** | **1.00** | **1.92 (± 0.51)** | **0.92, 2.92** | **6.82x (success >0/ success=0)** | **2.51, 18.53** |
| Receiver Success >0 | 0.67 | -0.43 (± 0.44) | -1.29, 0.43 | 0.65x (success >0/ success=0) | 0.27, 1.54 |
| Donor Age | 0.58 | -0.43 (± 0.51) | -1.43, 0.57 | 0.65x (juveniles/ non-juveniles) | 0.24, 1.77 |
| Food Familiarity | 0.46 | -0.19 (± 0.30) | -0.78, 0.40 | 0.83x (familiar/ novel) | 0.46, 1.49 |
| Receiver Age | 0.24 | 0.07 (± 0.19) | -0.30, 0.44 | 1.07x (juveniles/ non-juveniles) | 0.74, 1.56 |
| Receiver Sex | 0.10 | -0.02 (± 0.12) | -0.26, 0.22 | 0.98x (females/ males) | 0.77, 1.24 |

Although novel foods (i.e. novel at the start of the experiment) were more successfully transferred than familiar foods, the *food familiarity* variable had little effect in predicting the success of a transfer. With the *donor success* variable, however, we can see that transfers were more successful when the donor had at least one previous experience (ingestion) with the particular food being transferred (Fig. 5.3), than when it had previously never ingested that food type. Thus the donor first needs to know that the food is palatable before transferring it, or be familiar with the experimental set up.

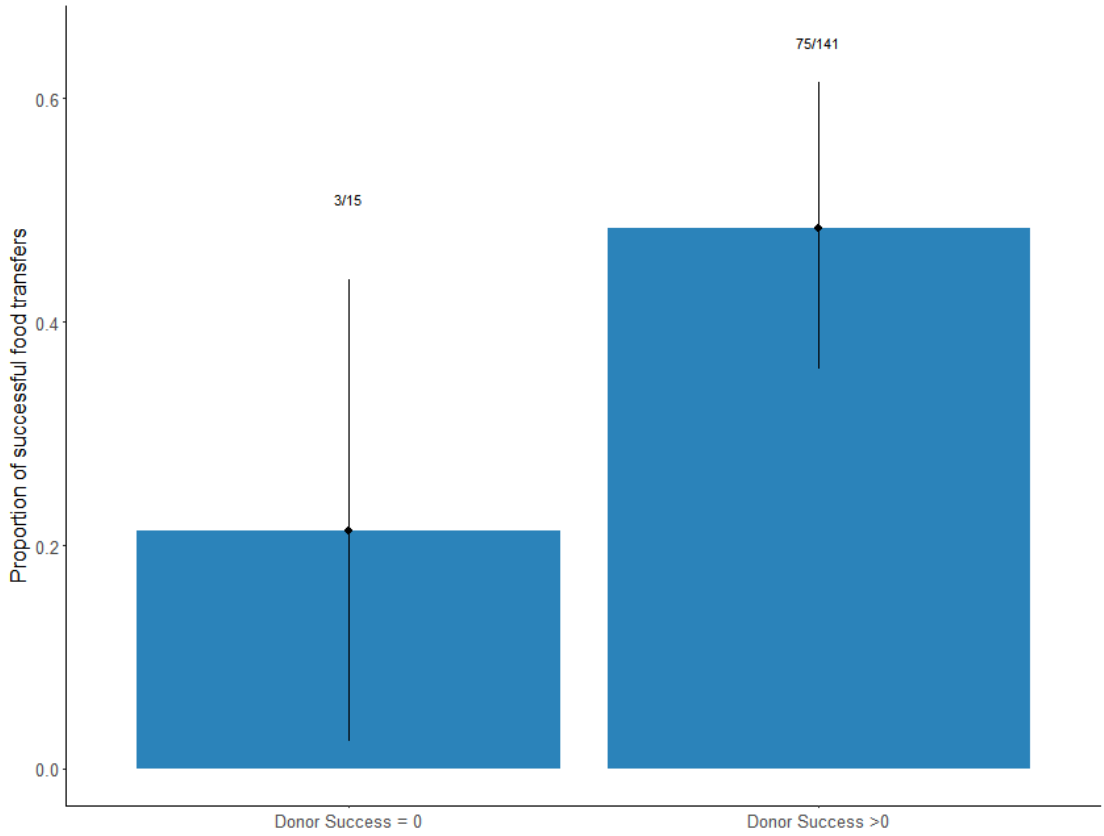


Figure 5.3: Proportion of success of food transfers for novel food, averaged by individuals, when the donor has not previously ingested the food type, and when it has. Error bars are 95% C.I., not assuming normality

In previous studies it was found that fathers were more involved in food transfers than other group members. Although I did not have the genetic data, we looked at the first model with an interaction between *age* and *sex*, but this interaction variable has a very low relative importance (3%), so I suspect that in this species the adult males do not transfer food more successfully than other group members.

I also ran a similar analysis but restricted the data to juveniles as receivers and non-juveniles as donors, because I expected that if there is any teaching, the transfers would mainly be from non-juveniles to juveniles. The top models fitted are shown in Table 5.9 and results of model averaging are in Table 5.10. Even within this dataset, the effect of *food familiarity* is still low (effect size = -0.16; 95% C.I. = -0.79, 0.47; Table 5.10), with familiar foods transferred 0.85 times less successfully than novel food (95% U.C.I. = 0.46-1.60). The *sex* of the *receiver* is the best predictor in this case (effect size = -0.57; 95% C.I. = -1.43,

0.29; Table 5.10), with juvenile females obtaining 0.57 times less successful transfers (95% U.C.I. = 0.24-1.34) than juvenile males (Table 5.10). However, all 95% C.I. for the parameter estimates in the top models included zero, so there is little evidence that any predictor variables affect transfer success.

Table 5.9: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (continuous) on the probability of success of food transfers, with juveniles as receivers and non-juveniles as donors (from 129 observations, of 10 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Receiver Sex | 4 | 183.27 | 0.00 | 0.17 |
| Food Familiarity + Receiver Sex | 5 | 183.85 | 0.58 | 0.12 |
| Null | 3 | 184.83 | 1.56 | 0.08 |

Table 5.10: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of a success of food transfers, with juveniles as receivers and non-juveniles as donors

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | 0.46 (± 0.36) | -0.25, 1.17 | 1.58 baseline odds of success | 0.78, 3.21 |
| Receiver Sex | 0.79 | -0.57 (± 0.44) | -1.43, 0.29 | 0.57x (females/ males) | 0.24, 1.34 |
| Food Familiarity | 0.34 | -0.16 (± 0.32) | -0.79, 0.47 | 0.85x (familiar/ novel) | 0.46, 1.60 |

As per the previous analysis, even though there was no continuous effect of novelty on the probability of success of a food transfer, it left the possibility that a single ingestion was sufficient for a food option to become familiar. I went on to test this by running the same analysis with the OSS variables as binary. The top models fitted are shown in Table 5.11 and results of model averaging are in Table 5.12. Similarly I found little effect of *food familiarity* (effect size = -0.18;

95% C.I. = -0.85, 0.49; Table 5.12) but results were in the same direction with familiar foods being transferred 0.84 times less successfully than novel food (95% U.C.I. = 0.43-1.63), and a similar effect of *receiver sex* (effect size = -0.59; 95% C.I. = -1.45, 0.27; Table 5.12) with juvenile females obtaining 0.55 times less successful transfers (95% U.C.I. = 0.23-1.31).

Table 5.11: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (binary) on the probability of success of food transfers, with juveniles as receivers and non-juveniles as donors (from 129 observations, of 10 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Receiver Sex | 4 | 183.27 | 0.00 | 0.13 |
| Donor Success >0 + Receiver Sex + Receiver Success >0 | 6 | 183.39 | 0.11 | 0.13 |
| Food Familiarity + Donor Success >0 + Receiver Sex + Receiver Success >0 | 7 | 183.60 | 0.33 | 0.11 |
| Donor Success >0 + Receiver Sex | 5 | 183.65 | 0.38 | 0.11 |
| Food Familiarity + Receiver Sex | 5 | 183.85 | 0.58 | 0.10 |
| Food Familiarity + Donor Success >0 + Receiver Sex | 6 | 184.09 | 0.81 | 0.09 |
| Receiver Sex + Receiver Success >0 | 5 | 184.28 | 1.01 | 0.08 |
| Donor Success >0 | 4 | 184.71 | 1.44 | 0.06 |
| Donor Success >0 + Receiver Success >0 | 5 | 184.78 | 1.51 | 0.06 |
| Food Familiarity + Receiver Sex + Receiver Success >0 | 6 | 184.80 | 1.52 | 0.06 |
| (Null) | 3 | 184.83 | 1.56 | 0.06 |

Table 5.12: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of a success of food transfers, with juveniles as receivers and non-juveniles as donors

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -0.20 (± 1.20) | -2.56, 2.15 | 0.82 baseline odds of success | 0.08, 8.60 |
| Receiver Sex | 0.81 | -0.59 (± 0.44) | -1.45, 0.27 | 0.55x (females/ males) | 0.23, 1.31 |
| Donor Success >0 | 0.56 | 0.96 (± 1.24) | -1.47, 3.39 | 2.61x (success >0/ success=0) | 0.23, 29.68 |
| Receiver Success >0 | 0.44 | -0.31 (± 0.48) | -1.25, 0.63 | 0.73x (success >0/ success=0) | 0.29, 1.88 |
| Food Familiarity | 0.36 | -0.18 (± 0.34) | -0.85, 0.49 | 0.84 x (familiar/ novel) | 0.43, 1.63 |

Although not the best predictor, novel foods are transferred with more success than familiar food, especially when the juveniles are receivers. Yet the importance of *food familiarity* in the models is low. The pattern of novel food transfer being more successful than familiar food might however not be linked to teaching behaviour. The pattern could be observed because juveniles attempt to obtain more novel food than familiar food, and are therefore responsible for this pattern. The pattern could also be due to the fact that adults, although they ingest those novel foods, prefer the familiar ones and are more likely to get rid of the novel foods.

#### 5.4.1.3 Probability of attempting a food transfer

I investigated the probability of juveniles attempting a food transfer from a non-juvenile when that individual was consuming food. The data were restricted to juveniles as potential receivers and adults/subadults as potential donors.

Table 5.13 shows the top models that predict the attempt of a food transfer from an adult to a juvenile. Table 5.14 shows the results of the model averaging. Only *receiver success* as a binary variable seems to predict the probability of attempting a food transfer. The other variables did not have any particular effect in predicting the attempt of food transfers. Particularly, *food familiarity* (Fig. 5.4) did not affect juvenile's attempts to get food (effect size = 0.09; 95% C.I. = -0.26, 0.44). Hence, the weak increase in successful food transfers for novel food, relative to familiar food, is unlikely to be a result of an increase in juveniles' motivation to obtain unfamiliar foods from non-juveniles. If anything, there is a slight indication that juveniles were more likely to attempt to obtain familiar, rather than unfamiliar food (see Table 4.13; Fig. 4.4).

Table 5.13: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (binary) on the probability of attempting a food transfer (from 1072 observations, of 10 potential receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Receiver Success >0 | 4 | 265.43 | 0.00 | 0.62 |
| Food Familiarity + Receiver Success >0 | 5 | 266.45 | 1.02 | 0.38 |

Table 5.14: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of attempting a food transfer

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of attempts | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -3.24 (± 0.40) | -4.02, -2.46 | 0.040 baseline odds of attempt | 0.02, 0.09 |
| **Receiver Success >0** | **1.00** | **1.13 (± 0.37)** | **0.40, 1.86** | **3.10x (success >0/ success=0)** | **1.50, 6.39** |
| Food Familiarity | 0.38 | 0.09 (± 0.18) | -0.26, 0.44 | 1.09x (familiar/ novel) | 0.77, 1.56 |

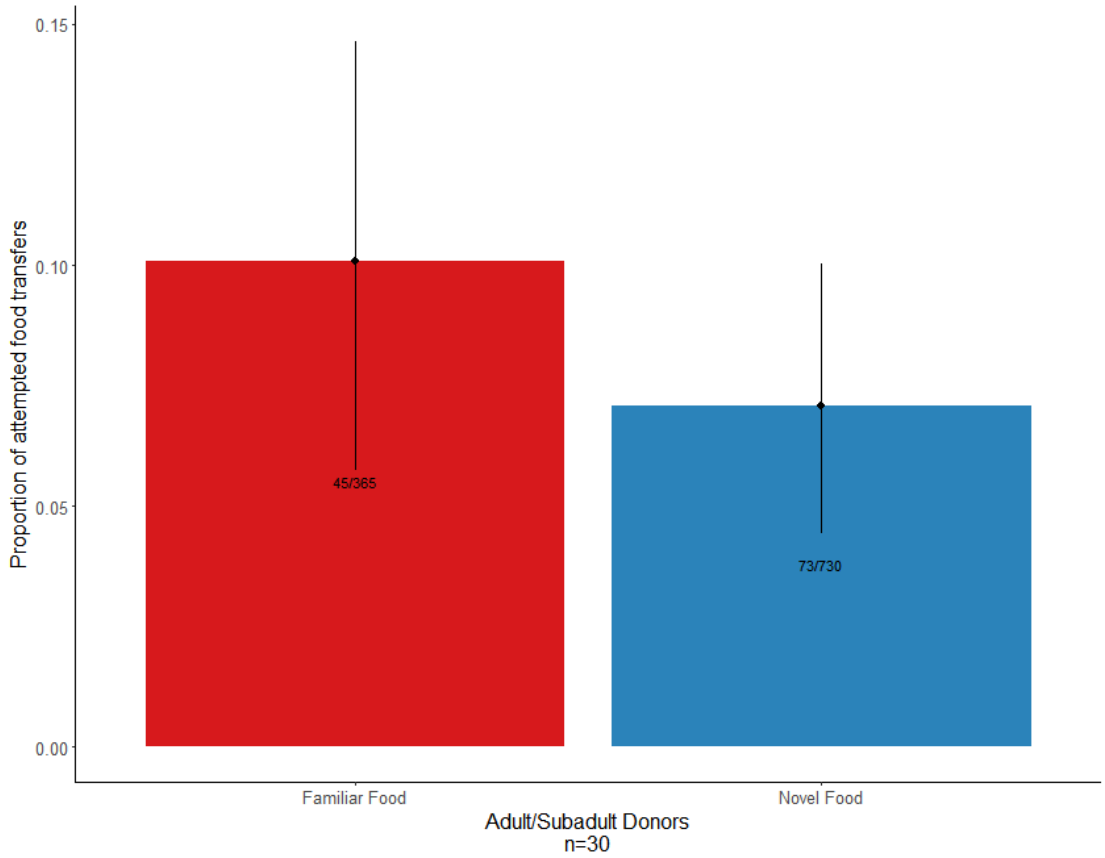


Figure 5.4: Barplot showing the effect of *food familiarity* on the proportion of attempted food transfers, averaged by individuals. Error bars are 95% C.I., not assuming normality

Although there was little evidence that juveniles attempt to obtain more or less food that was novel at the start of the experiment, there was an effect of having consumed a particular food type on the probability of attempting a food transfer in the context of the experiment. When the juveniles have had no previous experience (*receiver success* ==0) with a particular food option in the context of this experiment, the probability that they attempt to obtain food is lower than once they have had previous ingestion of the respective food option (effect size = 1.13; 95% C.I. = 0.40, 1.86). In fact, when a juvenile has already ingested a specific type of food it is 3.10 times (95% U.C.I. = 1.50-6.39) more likely to attempt to obtain it than when it has never ingested it (Table 5.14; Fig. 5.5).

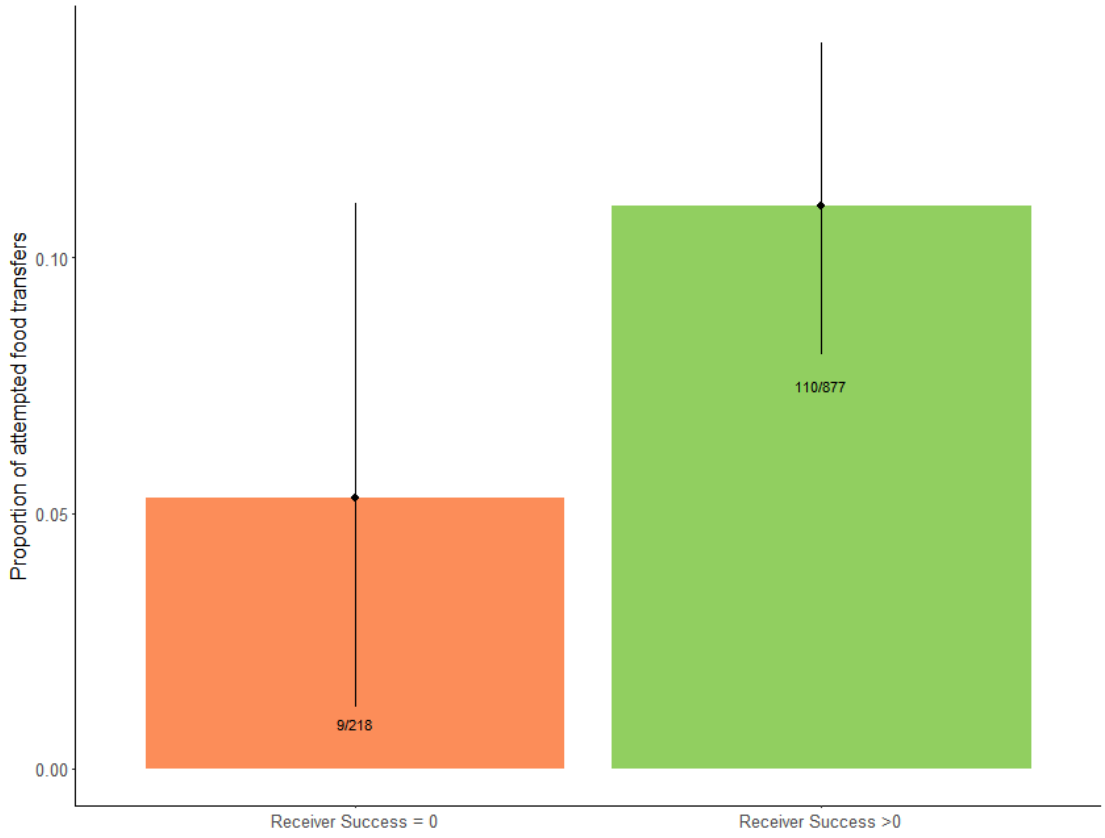


Figure 5.5: Barplot showing the effect of *receiver success* (as binary) on the proportion of attempted food transfers, averaged by individuals, with both food types combined. Error bars are 95% C.I, not assuming normality

#### 5.4.1.4 Probability of resistance (during a transfer)

I then wanted to look at the involvement of the donor in determining the probability that a food transfer would be successful. As a proxy of the donor's preference for keeping versus giving up food items, I used resistance during a food transfer to see if donors were more likely to give up novel food relative to familiar food.

70% of all food transfers were resisted by the donor (Table 5.15; Fig. 5.6), and this dropped to 62% when juveniles are receivers and adults/subadults were donors (Table 5.16).

Table 5.15: Resistance in failed and successful food transfers (for all food transfers)

| Transfer | Fail | Success |
|---|---|---|
| Resistance | 100 | 61 |
| No Resistance | 20 | 49 |
| Unknown | 2 | 1 |

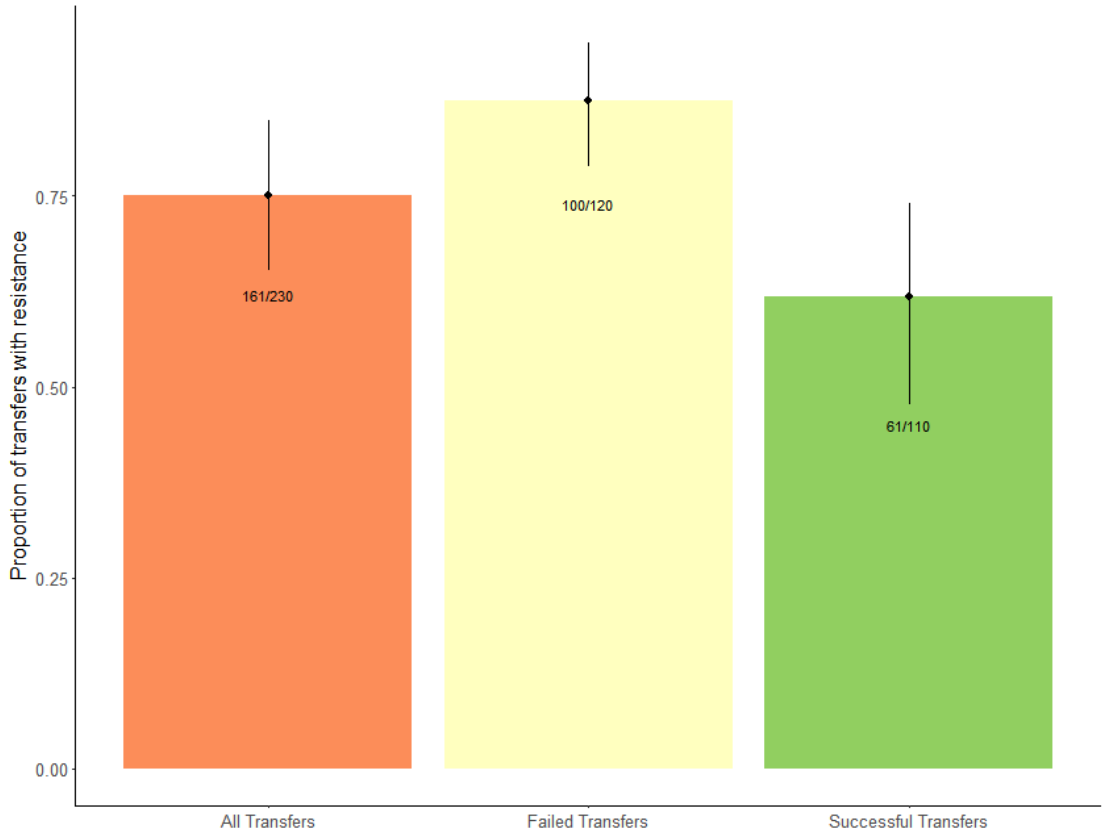


Figure 5.6: Barplot showing the proportion of resistance in food transfers, averaged by individuals. Error bars are 95% C.I., not assuming normality

Table 5.16: Resistance in failed and successful food transfers with juvenile receivers and adult/subadult donors only

| Transfer | Fail | Success |
|---|---|---|
| Resistance | 43 | 30 |
| No Resistance | 12 | 32 |
| Unknown | 2 | 1 |

In the following models, the data were restricted to juveniles as potential receivers and adults/subadults as potential donors. Table 5.17 shows the top models that predict the resistance in food transfers from an adult to a juvenile. Table 5.18 shows the results of the model averaging. No variable had a particular importance in predicting resistance to a food transfer. In particular, there was little evidence that adults/subadults were more or less likely to give up food that was novel at the start of the experiment (*food familiarity* effect size = 0.53; 95% C.I. = -0.69, 1.75). Likewise, there was little evidence that the probability of resistance was a function of the number of times the potential donor or recipient had already consumed the food type in the experimental

context (*donor success* effect size = -0.002, 95% C.I. = -0.02, 0.02; *receiver success* is not in the top models).

Table 5.17: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (continuous) on the probability of resisting a food transfer (from 117 observations, of 32 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Food Familiarity | 4 | 149.86 | 0.00 | 0.28 |
| Null | 3 | 150.10 | 0.24 | 0.25 |
| Food Familiarity + Receiver Sex | 5 | 150.36 | 0.50 | 0.22 |
| Receiver Sex | 4 | 151.03 | 1.17 | 0.15 |
| Food Familiarity + Donor Success | 5 | 151.81 | 1.95 | 0.10 |

Table 5.18: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of resisting a food transfer

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | 0.63 (± 0.55) | -0.45, 1.71 | 1.88 baseline odds of resistance | 0.63, 5.52 |
| Food Familiarity | 0.60 | 0.53 (± 0.62) | -0.69, 1.75 | 1.70x (familiar/ novel) | 0.50, 5.73 |
| Receiver Sex | 0.37 | 0.25 (± 0.47) | -0.67, 1.17 | 1.28x (females/ males) | 0.51, 3.23 |
| Donor Success | 0.10 | -0.002 (± 0.01) | -0.02, 0.02 | 1.00x per previous success | 0.98, 1.02 |

Similar to the model above looking at success of food transfers, I wanted to investigate the effect of *receiver success* and *donor success* as binary variables on the resistance during a food transfer (i.e. eaten versus not eaten food type in the experimental context). Table 5.19 shows the top models that predict the resistance in food transfers from an adult to a juvenile with *receiver success* and *donor success* as binary variables. Table 5.20 shows the results of the model averaging. The pattern showed by the *food familiarity* variable suggests that non-

juveniles resist more for familiar food than for novel food, but the pattern showed by the *donors' previous success* variable suggests that they resist more when they have no experience with the food option. However, overall, as per the previous model, neither the *food familiarity* at the start of the experiment (effect size = 0.60; 95% C.I. = -0.71, 1.91; Table 5.20; Fig. 5.7) nor the *donor's previous success* during the experiment predicted resistance (effect size = -1.29; 95% C.I. = -4.50, 1.92; Table 5.20; Fig. 5.8). Hence adults/subadults seemed equally likely to resist attempted food transfers by juveniles whether the food was novel or familiar, and also equally likely to resist when they have already had an experience with the food option compared to when they have not.

Table 5.19: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (binary) on the probability of resisting a food transfer (from 117 observations, of 32 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Food Familiarity + Donor Success >0 + Receiver Success >0 | 6 | 149.35 | 0.00 | 0.12 |
| Food Familiarity + Donor Success >0 + Receiver Sex + Receiver Success >0 | 7 | 149.80 | 0.45 | 0.09 |
| Food Familiarity | 4 | 149.86 | 0.51 | 0.09 |
| Food Familiarity + Donor Success >0 | 5 | 149.98 | 0.63 | 0.08 |
| Donor Success >0 + Receiver Success | 5 | 150.04 | 0.69 | 0.08 |
| (Null) | 3 | 150.10 | 0.74 | 0.08 |
| Food Familiarity + Receiver Sex | 5 | 150.36 | 1.00 | 0.07 |
| Food Familiarity + Donor Success >0 + Receiver Sex | 6 | 150.51 | 1.16 | 0.07 |
| Donor Success >0 | 4 | 150.58 | 1.23 | 0.06 |
| Food Familiarity + Receiver Success >0 | 5 | 150.75 | 1.40 | 0.06 |
| Receiver Success >0 | 4 | 150.96 | 1.61 | 0.05 |
| Receiver Sex | 4 | 151.03 | 1.68 | 0.05 |
| Donor Success >0 + Receiver Sex + Receiver Success >0 | 6 | 151.07 | 1.72 | 0.05 |
| Food Familiarity + Receiver Sex + Receiver Success >0 | 6 | 151.26 | 1.90 | 0.04 |

Table 5.20: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of resisting a food transfer

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | 1.48 (± 1.53) | -1.52, 4.48 | 4.39 baseline odds of resistance | 0.22, 88.13 |
| Food Familiarity | 0.62 | 0.60 (± 0.67) | -0.71, 1.91 | 1.82x (familiar/ novel) | 0.49, 6.77 |
| Donor Success >0 | 0.55 | -1.29 (± 1.64) | -4.50, 1.92 | 0.28x (success >0/ success=0) | 0.01, 6.85 |
| Receiver Success >0 | 0.50 | 0.47(± 0.64) | -0.78, 1.72 | 1.60 x (success >0/ success=0) | 0.46, 5.61 |
| Receiver Sex | 0.37 | 0.27 (± 0.49) | -0.69, 1.23 | 1.31x (females/ males) | 0.50, 3.42 |

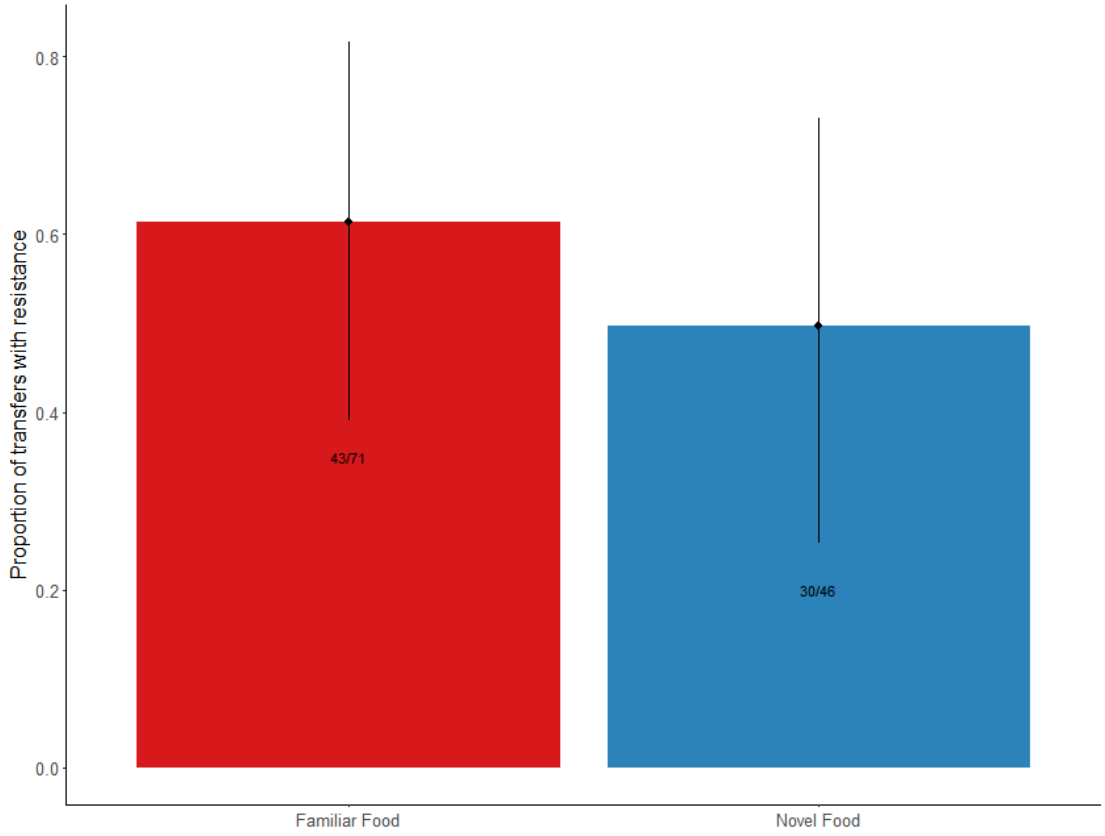


Figure 5.7: Barplot showing the effect of *food familiarity* on the proportion of resistance in food transfers, averaged by individuals. Donors are adults/subadults, n=25. Error bars are 95% C.I., not assuming normality

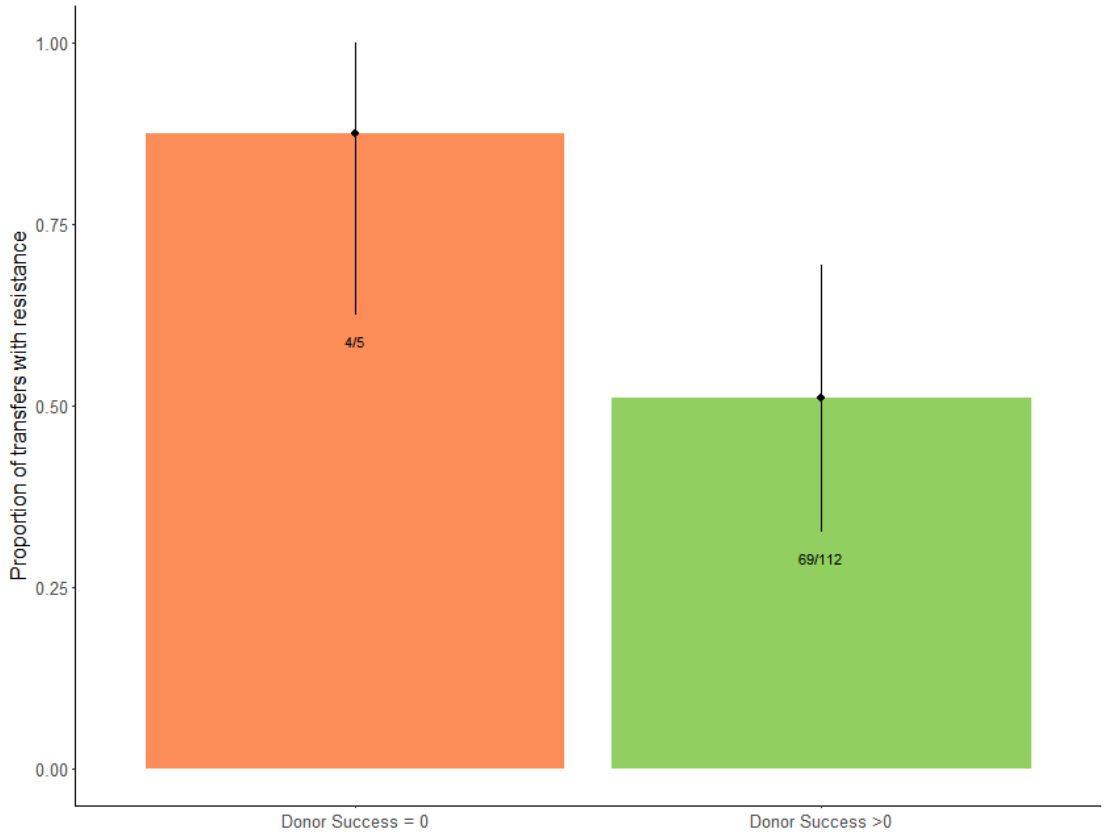


Figure 5.8: Barplot showing the effect of *donor success* as a binary variable on the proportion of resistance in food shares, averaged by individuals. Donors are adults/subadults, n=25. Error bars are 95% C.I., not assuming normality

#### 5.4.1.5 Probability of succeeding in a food transfer, given resistance

Finally I wanted to know if, despite the resistance during food transfers, juveniles were more motivated to obtain novel food compared to familiar food once they were engaged in a transfer. I selected the data of all the food transfers that had some resistance, and re-analysed the probability of success in those food transfers. I did that for all food transfers, not just the ones that were from adults/subadults to juveniles. As per the previous models I fitted models both with *receiver success* and *donor success* as continuous variables (Table 5.21 and 5.22) and as binary variables (Table 5.23 and 5.24). The *age of the receiver* was not a good predictor of probability of success in a food transfer given resistance (effect size = 0.07; 95% C.I. -0.32, 0.46, Table 5.22). Juveniles were therefore not more likely to successfully obtain food from a transfer than adults when there was resistance on the part of the donor. However, previous successes as binary variables were better predictors. Food transfers were more successful if the

donor had previous experience with the food option (effect size = 1.72; 95% C.I. = 0.52, 3.39; Table 5.24) or if the receiver had no previous success with the food option (effect size = -0.70; 95% C.I. = -1.78, 0.38; Table 5.24). This supports the teaching hypothesis as food items are more likely transferred, despite resistance, from knowledgeable individuals to unknowledgeable individuals.

Table 5.21: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (continuous) on the probability of success of food transfers when there was resistance (from 161 observations, of 32 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Null | 3 | 219.80 | 0.00 | 0.33 |
| Receiver Age | 4 | 220.75 | 0.94 | 0.20 |
| Receiver Success | 4 | 221.08 | 1.28 | 0.17 |
| Donor Age | 4 | 221.19 | 1.38 | 0.16 |
| Donor Success | 4 | 221.66 | 1.86 | 0.13 |

Table 5.22: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of success of food transfers when there was resistance

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -0.51(± 0.23) | -0.96, -0.06 | 0.60 baseline odds of success | 0.38, 0.94 |
| Receiver Age | 0.20 | 0.07 (± 0.20) | -0.32, 0.46 | 1.07x (juveniles/ non-juveniles) | 0.72, 1.59 |
| Receiver Success | 0.17 | -0.003 (± 0.01) | -0.02, 0.02 | 1.00x per previous success | 0.98, 1.02 |
| Donor Age | 0.16 | -0.06 (± 0.22) | -0.49, 0.37 | 0.94x (juveniles/ non-juveniles) | 0.61, 1.45 |
| Donor Success | 0.13 | 0.002 (± 0.01) | -0.02, 0.02 | 1.00x per previous success | 0.98, 1.02 |

Table 5.23: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (binary) on the probability of success of food transfers when there was resistance (from 161 observations, of 32 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Donor Success >0 + Receiver Success >0 | 5 | 216.50 | 0.00 | 0.37 |
| Donor Age + Donor Success >0 + Receiver Success >0 | 6 | 217.18 | 0.68 | 0.26 |
| Donor Success >0 | 4 | 217.77 | 1.26 | 0.20 |
| Donor Success >0 + Receiver Age + Receiver Success >0 | 6 | 218.07 | 1.57 | 0.17 |

Table 5.24: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of success of food transfers when there was resistance

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -1.51 (± 0.81) | -3.10, 0.08 | 0.22 baseline odds of success | 0.05, 1.08 |
| **Donor Success >0** | **1.00** | **1.72 (± 0.85)** | **0.52, 3.39** | **5.58x (success >0/ success=0)** | **1.06, 29.55** |
| Receiver Success >0 | 0.80 | -0.70 (± 0.55) | -1.78, 0.38 | 0.50x (success >0/ success=0) | 0.17, 1.46 |
| Donor Age | 0.26 | -0.14 (± 0.34) | -0.81, 0.53 | 0.87x (juvenile/ non-juveniles) | 0.45, 1.69 |
| Receiver Age | 0.17 | 0.04 (± 0.17) | -0.29, 0.37 | 1.04x (juveniles/ non-juveniles) | 0.75, 1.45 |

The same analysis was fitted restricting the transfers to those with juveniles as receivers and non-juveniles as donors (Tables 5.25-28). Juveniles were not more likely to obtain novel foods compared to familiar ones during food transfers in which non-juvenile donors were resisting, and there was little

evidence that *food familiarity* affected the success of food transfers (effect size = -0.05; 95% C.I. = -0.50, 0.40, Table 5.26).

Table 5.25: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (continuous) on the probability of success of food transfers when there was resistance, with juveniles as receivers and non-juveniles as donors (from 73 observations, of 9 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Null | 3 | 105.22 | 0.00 | 0.43 |
| Donor Success | 4 | 106.46 | 1.24 | 0.23 |
| Donor Sex | 4 | 106.99 | 1.77 | 0.18 |
| Food Familiarity | 4 | 107.05 | 1.83 | 0.17 |

Table 5.26: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of success of food transfers when there was resistance, with juveniles as receivers and non-juveniles as donors

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -0.43 (± 0.33) | -1.08, 0.22 | 0.65 baseline odds of success | 0.34, 1.24 |
| Donor Success | 0.23 | 0.01 (± 0.03) | -0.05, 0.07 | 1.01x per previous success | 0.95, 1.07 |
| Donor Sex | 0.18 | 0.06 (± 0.24) | -0.41, 0.53 | 1.06x (females/ males) | 0.66, 1.70 |
| Food Familiarity | 0.17 | -0.05 (± 0.23) | -0.50, 0.40 | 0.95x (familiar/ novel) | 0.61, 1.49 |

Table 5.27: GLMM to investigate the effect of food familiarity, individuals' age and sex, and previous success (binary) on the probability of success of food transfers when there was resistance, with juveniles as receivers and non-juveniles as donors (from 73 observations, of 9 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Donor Success >0 | 3 | 103.07 | 0.00 | 0.25 |
| Donor Success >0 + Receiver Success >0 | 4 | 103.11 | 0.05 | 0.25 |
| Donor Sex + Donor Success >0 | 4 | 103.99 | 0.92 | 0.16 |
| Donor Sex + Donor Success >0 + Receiver Succcess >0 | 4 | 104.41 | 1.35 | 0.13 |
| Food Familiarity + Donor Success >0 | 5 | 104.74 | 1.68 | 0.11 |
| Food Familiarity + Donor Success >0 + Receiver Success >0 | 5 | 10.79 | 1.73 | 0.11 |

Table 5.28: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of success of food transfers when there was resistance, with juveniles as receivers and non-juveniles as donors

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -17.34 (±1058.58) | -2092, 2057 | 0 baseline odds of success | 0, Inf |
| Donor Success >0 | 1.00 | 17.50 (± 1058.58) | -2057, 2092 | Infx (success >0/ success=0) | 0, Inf |
| Receiver Success >0 | 0.48 | -0.52 (± 0.76) | -2.01, 0.97 | 0.59x (success >0/ success=0) | 0.13, 2.64 |
| Donor Sex | 0.29 | 0.16 (± 0.37) | -0.57, 0.89 | 1.17x (females/ males) | 0.57, 2.42 |
| Food Familiarity | 0.22 | -0.09 (± 0.29) | -0.66, 0.48 | 0.91x (familiar/ novel) | 0.52, 1.61 |

Similar to the analysis of the probability of success in all food transfers (5.4.1.2), *donor success* as a binary variable had an important impact on the probability of success of a food transfers in which the donor is resisting. Hence, even if the donor was resisting the transfers, if it had prior experience with that

food type, then the transfer was more likely to succeed than if the donor had no previous experience with that food type, however individual variation was high.

#### 5.4.1.6 Probability of succeeding in a food transfer in the second phase of the experiment

Four juveniles were born between the first and second phase, which allowed me to investigate how prior-adult sampled food would be transferred compared to novel and familiar food. In the second phase of the experiment, there were 163 food transfers, of which 51 were successful (31%) and 48 led to eating transferred food (29% of all transfers) (in three transfers the receiver obtained food but did not eat it). There were 4313 foraging related events (explore, eat, scrounge, food transfer), of which 1% were food transfers. 3% of the ingestion events were from food transfers (1465 ingestion events). 18% of the successful food transfers were made with novel food, 61% with PAS prior-adult sampled food, and 21% with familiar food (Table 5.29). Similar to the first phase, insects were rarely sampled, and never transferred.

Table 5.29: Successful and failed transfer for each type of food, in the second phase of the experiment

| Transfer | Apple | Banana (Fam) | Cricket | Grape | Mealworm | Papaya | Pear |
|---|---|---|---|---|---|---|---|
| Fail | 20 | 28 | 0 | 41 | 0 | 3 | 20 |
| Success | 4 | 11 | 0 | 27 | 0 | 0 | 9 |

When only juvenile receivers were selected, there were only 13/57 (23%) successful food transfers made to the four juveniles. Two successful and four unsuccessful transfers were between juveniles, while three successful and six unsuccessful transfers involved an unknown donor. There was also one successful transfer that did not lead to eating transferred food. Table 5.30 shows the raw data from food transfers with juvenile recipients and adult/subadult donors. This data also include the transfers whose donors were unknown adults. In this case 27% of the successful food transfers were made with novel food, 55% with prior-adult sampled food, and 18% with familiar food (Table 5.30).

Table 5.30: Successful and failed transfer for each type of food for juvenile recipients and adult/subadults donors only, in the second phase of the experiment

| Transfer | Apple | Banana (Fam) | Cricket | Grape | Mealworm | Papaya | Pear |
|---|---|---|---|---|---|---|---|
| Fail | 11 | 9 | 0 | 14 | 0 | 0 | 4 |
| Success | 3 | 2 | 0 | 3 | 0 | 0 | 3 |

The difference in the number of transfers from the first phase (129 food transfers) to the second phase (57 food transfers) towards juveniles is unlikely to be due to a decrease of activity between the first and second phase, because 3506 foraging related events occurred in the first phase and 4313 in the second phase. There was also an average of 12.9 food transfers per juveniles in the first phase and 14.25 in the second phase. In fact, per juvenile, there were more food transfers in the second phase than in the first one.

Based on the analysis of the first phase, and because the AICc values of the models were lower than those for models with *donor* and *receiver success* as continuous variables, here I report only models with *donor* and *receiver success* as binary variables. In this analysis, because I was interested in the effect of prior-adult sampled foods, I ran the analysis with the *novelty* variable as binary: the food was either prior-adult sampled food or not (familiar or novel). Table 5.31 shows the top models that predict the success of a food transfer for all individuals in the second phase, and Table 5.32 shows the results of the model averaging. For the four juveniles in the second phase of the experiment, the *food novelty* (prior-adult sampled or not) seemed to have little impact on the success of a transfer (effect size = 0.03; 95% C.I. = -0.26, 0.32; Table 5.32). Prior-adult sampled foods had 1.03 more chance to be successfully transferred than non-prior-adult sampled foods (95% U.C.I = 0.77-1.38). *Donor sex* however had an important effect (effect size = 0.83; 95% C.I. = 0.09, 1.57; Table 5.32), with females being 2.29 times more likely to transfer food than males (95% U.C.I = 1.09, 4.83).

Table 5.31: GLM to investigate the effect of PAS, individuals' age and sex, and previous success (binary) on the probability of success of food transfers (from 148 observations, of 41 receivers within 6 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Donor Sex + Donor Success >0 + Receiver Age | 4 | 180.48 | 0.00 | 0.34 |
| Donor Sex + Donor Success >0 + Novelty + Receiver Age | 5 | 182.33 | 1.85 | 0.14 |
| Donor Sex + Donor Success >0 + Receiver Age + Receiver Success >0 | 5 | 182.38 | 1.89 | 0.13 |
| Donor Sex + Donor Age + Donor Success >0 + Receiver Age | 5 | 182.39 | 1.90 | 0.13 |
| Donor Sex + Receiver Age | 3 | 182.42 | 1.93 | 0.13 |
| Donor Sex + Donor Success >0 | 3 | 182.43 | 1.94 | 0.13 |

Table 5.32: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of success of food transfers

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -2.50 (± 1.21) | -4.87, 0.13 | 0.08 baseline odds of success | 0.01, 0.88 |
| **Donor Sex** | **1.00** | **0.83 (± 0.38)** | **0.09, 1.57** | **2.29x (females/ males)** | **1.09, 4.83** |
| Donor Success >0 | 0.87 | 1.55 (± 1.17) | -0.74, 3.84 | 4.71x (success >0/ success=0) | 0.48, 46.67 |
| Receiver Age | 0.87 | -0.72 (± 0.49) | -1.68, 0.24 | 0.18x (juveniles/ non-juveniles) | 0.07, 0.47 |
| Novelty (==PAS) | 0.14 | 0.03 (± 0.15) | -0.26, 0.32 | 1.03x (PAS/ familiar or novel) | 0.77, 1.38 |
| Receiver Success >0 | 0.13 | 0.03 (± 0.20) | -0.36, 0.42 | 1.03x (success >0/ success=0) | 0.70, 1.53 |
| Donor Age | 0.13 | -0.04 (± 0.23) | -0.49, 0.41 | 0.96x (juveniles/ non-juveniles) | 0.61, 1.51 |

A similar analysis was carried out with only juveniles as receivers and non-juveniles as donors, with Table 5.33 and 5.34 showing the results for the top models. Again, there was little evidence for an effect of *novelty* (effect size = -0.32; 95% C.I. = -1.59, 0.95). When back-transforming some 95% confidence intervals, the values obtained range from zero to infinity, because the model was probably not able to estimate the standard errors effectively, potentially due to small sample sizes.

Table 5.33: GLM to investigate the effect of PAS, individuals' age and sex, and previous success (binary) on the probability of success of food transfers, with juveniles as receivers and non-juveniles as donors (from 40 observations, of 4 receivers within 2 groups). The table shows the top models, with the number of estimable parameters (Df), AICc values, Δ AIC and Akaike weights ($\omega_i$) (support for models)

| Model | Df | AICc | Δ AIC | $\omega_i$ |
|---|---|---|---|---|
| Null | 1 | 42.14 | 0.00 | 0.34 |
| Novelty | 2 | 43.12 | 0.98 | 0.21 |
| Donor Success >0 | 2 | 43.44 | 1.30 | 0.18 |
| Receiver Success >0 | 2 | 43.66 | 1.52 | 0.16 |
| Donor Success >0 + Novelty | 3 | 44.07 | 1.93 | 0.13 |

Table 5.34: Table showing the relative importance (sum of Akaike weights), estimates, unconditional standard errors, back-transformed effect on odds of success and their confidence intervals for parameters included in the top models predicting the probability of success of food transfers, with juveniles as receivers and non-juveniles as donors

| Variable | Sum of weights | Model averaged estimate (± unconditional SE) | 95% C.I. | Back-transformed effect on odds of success | Back-transformed unconditional 95% C.I. |
|---|---|---|---|---|---|
| Intercept | | -6.27 (± 1539.36) | -3023, 3011 | 0.002 baseline odds of success | 0 - Inf |
| Novelty (==PAS) | 0.33 | -0.32 (± 0.65) | -1.59, 0.95 | 0.73x (PAS/ familiar or novel) | 0.20-2.60 |
| Donor Success >0 | 0.30 | 4.99 (± 1539.36) | -3012, 3022 | 146.94x (success >0/ success=0) | 0 - Inf |
| Receiver Success >0 | 0.16 | 0.11 (± 0.44) | -0.75, 0.97 | 1.12x (success >0/ success=0) | 0.47-2.64 |

When analysing the effect of food types based on the familiar, prior-adult sampled and novel classification, there seemed to be some small differences in the results when restricting the data to transfers from non-juveniles to juveniles (Table 5.32 and 5.34).

### 5.4.2 Third criterion: Learning

#### 5.4.2.1 Hypothesis testing

To investigate the role of food transfers in juveniles' foraging choices, I first applied a hypothesis testing model selection as suggested by McElreath (2016). For the "teaching" hypothesis, only *successful food transfers* were included as predictors (H1). I compared this to a non-teaching hypothesis, which included *eating*, *exploration*, *scrounging* and *observation* events (H2). The second "teaching" hypothesis was that *successful food transfers* would have an effect on juveniles' choices over and above other previous experience, so to test that the model included *eating*, *exploration*, *scrounging*, *observation* and *successful food transfers* (H1.bis). I also tested for asocial learning by only including *eating* and *exploration* in the model (H3), and for a social learning only model without teaching by including only *scrounging* and *observation* in the model (H4). However, it is questionable how social *scrounging* events are, so as an alternative social learning model without teaching I incorporated only *observation* as a parameter (H4.bis). Table 5.35 shows the results of the models corresponding to all six hypotheses. WAIC is the Widely Applicable Information Criterion, while P_WAIC is the effective number of parameters calculated to penalise the models (Watanabe, 2013; Whalen & Hoppitt, 2016). PARS is the actual number of parameters in each model, and LP is the log likelihood of the observations conditioned on the posterior parameters which quantifies how much each model match the data (Stan Development Team, 2016).

Table 5.35: Model fit results for hypothesis testing. Green cells show parameters for which the 95% credible interval does not overlap with zero

| Parameters/ Stats | Model Fit Results (H1) | 95% Credible Interval | Model Fit Results (H2) | 95% Credible Interval | Model Fit Results (H1.bis) | 95% Credible Interval |
|---|---|---|---|---|---|---|
| WAIC | 111.39 | | 116.11 | | 115.236 | |
| LP | -54.81 | | -55.10 | | -52.59 | |
| P_WAIC | 4.48 | | 8.02 | | 11.04 | |
| PARS | 7 | | 10 | | 11 | |
| $a_{apple}$ | -2.31 | -4.21, -0.86 | -3.14 | -5.44, -1.44 | -4.42 | -8.45, -1.63 |
| $a_{grape}$ | 0.27 | -0.51, 1.05 | -0.94 | -2.35, 0.30 | -1.09 | -2.56, 0.29 |
| $a_{pear}$ | -0.40 | -1.45, 0.57 | -0.94 | -2.42, 0.34 | -0.24 | -1.99, 1.57 |
| $a_{cricket}$ | -80.67 | -223.23, -5.56 | -82.34 | -220.17, -7.62 | -82.17 | -224.15, -7.58 |
| $a_{mealworm}$ | -82.41 | -224.97, -6.27 | -83.06 | -231.68, -6.90 | -84.11 | -224.43, -7.42 |
| $a_{papaya}$ | -80.76 | -229.63, -5.39 | -80.22 | -220.16, -6.41 | -83.16 | -226.48, -5.95 |
| $\beta_{eat}$ | - | - | -0.07 | -0.34, 0.19 | -0.29 | -0.74, 0.07 |
| $\beta_{explore}$ | - | - | 0.14 | -0.12, 0.40 | 0.39 | 0.03, 0.87 |
| $\beta_{scrounging}$ | - | - | 0.16 | -0.37, 0.75 | 0.37 | -0.28, 1.09 |
| $\beta_{SFT}$ | 0.15 | -0.06 0.37 | - | - | 0.42 | 0.11, 0.78 |
| $\beta_{observation}$ | - | - | -0.04 | -0.13, 0.03 | -0.12 | -0.23, -0.02 |

| Parameters/ Stats | Model Fit Results (H3) | 95% Credible Interval | Model Fit Results (H4) | 95% Credible Interval | Model Fit Results (H4.bis) | 95% Credible Interval |
|---|---|---|---|---|---|---|
| WAIC | 112.59 | | 114.91 | | 112.98 | |
| LP | -54.63 | | -56.21 | | -55.70 | |
| P_WAIC | 5.75 | | 5.15 | | 4.35 | |
| PARS | 8 | | 8 | | 7 | |
| $a_{apple}$ | -2.65 | -4.63, -1.16 | -2.58 | -4.65, -1.08 | -2.51 | -4.35, -1.04 |
| $a_{grape}$ | -0.44 | -1.36, 0.42 | 0.03 | -0.74, 0.77 | -0.03 | -0.72, 0.58 |
| $a_{pear}$ | -0.57 | -1.75, 0.54 | -0.62 | -1.83, 0.47 | -0.65 | -1.72, 0.40 |
| $a_{cricket}$ | -78.64 | -216.61, -5.86 | -80.44 | -220.72, -5.92 | -81.56 | -227.28, -6.07 |
| $a_{mealworm}$ | -82.79 | -224.48, -6.09 | -84.49 | -229.89, -6.81 | -81.68 | -233.93, -5.55 |
| $a_{papaya}$ | -81.71 | -225.60, -6.86 | -83.25 | -227.23, -5.61 | -81.04 | -222.37, -5.92 |
| $\beta_{eat}$ | 0.01 | -0.22, 0.24 | - | - | - | - |
| $\beta_{explore}$ | 0.03 | -0.17, 0.25 | - | - | - | - |
| $\beta_{scrounging}$ | - | - | -0.04 | -0.47, 0.38 | - | - |
| $\beta_{SFT}$ | - | - | - | - | - | - |
| $\beta_{observation}$ | - | - | 0.01 | -0.04, 0.05 | 0.01 | -0.02, 0.04 |

When comparing hypotheses, the best fitting model was the one with *successful food t*ransfers (H1). Moreover, when adding the *successful food transfers* parameter to a model with other potential learning parameters, I obtained a better fit (H1.bis's WAIC is lower than H2's). Combining those results suggests that eating food items that were obtained from a food transfer played an important role in the juveniles' future foraging decision, but the fact that in model H1, the credible interval overlapped with zero suggests that *successful food transfers* act in combination with other previous experience parameters, because its credible interval did not overlap with zero in H1.bis.

Adding *successful food transfers* to the non-teaching model improved the fit. However, the fit was not better than the baseline, where no $\beta$ (previous

experience parameters) were present (Table 5.36). This means that the search for the best model needs to be more refined, to see if another model with any parameter combination is a better fit than the baseline. In order to do this, I further used four model selection methods, with one looking at the full model and the parameters straddling zero, two were stepwise based on WAIC values, and another method was based on the uncertainty of the parameter.

Table 5.36: Model fit results for model without betas. Green cells show parameters for which the 95% credible interval does not overlap with zero

| Parameters/Stats | Model Fit Results | 95% Credible Interval |
|---|---|---|
| WAIC | 111.02 | |
| LP | -55.24 | |
| P_WAIC | 3.33 | |
| PARS | 6 | |
| $a_{apple}$ | -2.39 | -4.23, -0.97 |
| $a_{grape}$ | 0.001 | -0.70, 0.66 |
| $a_{pear}$ | -0.78 | -1.66, 0.37 |
| $a_{cricket}$ | -82.41 | -224.00, -6.88 |
| $a_{mealworm}$ | -79.92 | -214.85, -6.31 |
| $a_{papaya}$ | -82.33 | -226.35, -6.63 |

#### 5.4.2.2 Full model and "straddle" method

When running the full model, the MCMC chains converged and mixed well (see Appendix 5.B). When fitting the model including all parameters, all of the initial associations ($a$) except that of pear were different from that of banana (Table 5.37). The *initial association* for pear might not be different from that of banana because there was no previous experience with that food. Although this is also true for papaya, the juveniles never chose papaya in the first trial of the second phase. In fact, the *initial association* for cricket, mealworm and papaya are highly negative, which could be explained by the fact that they are never sampled in the first trial of the second phase. Apples and grapes were also slightly less preferred than bananas. *Explore* and *successful food transfers* seemed to be the best predictor of a juvenile's future choice, since their 95% credible interval does not overlap with zero. Hence the more juveniles explored a food type in the first phase of the experiment, the more likely they were to choose to eat that food in the first trial of the second phase, and the more they ate a food

from a successful food transfer in the first phase, the more likely they were to choose this food (Table 5.37). However, when fitting a model with only those two parameters, the 95% C.I. for *explore* and *successful food transfers* overlapped with zero, suggesting, that a more detailed analysis of the relationship between all the parameters is necessary. Moreover, because there are many parameters compared to the size of the data set, there are risks of overfitting. I therefore wanted to make the model as simple as possible in order to obtain more generalizable results.

Table 5.37: Model fit results for full model and "straddle" model. Green cells show parameters for which the 95% credible interval does not overlap with zero

| Parameters/ Stats | Model Fit Results (all parameters) | 95% Credible Interval | Model Fit Results (only explore and successful food transfer) | 95% Credible Interval |
|---|---|---|---|---|
| WAIC | 117.93 | | 110.01 | |
| LP | -52.32 | | -53.58 | |
| P_WAIC | 13.407 | | 5.42 | |
| PARS | 12 | | 8 | |
| $a_{apple}$ | -4.93 | -9.20, -1.98 | -2.50 | -4.44, -1.07 |
| $a_{grape}$ | -1.62 | -3.23, -0.04 | -0.19 | -1.14, 0.71 |
| $a_{pear}$ | -0.50 | -2.45, 1.37 | -0.14 | -1.23, 0.90 |
| $a_{cricket}$ | -80.23 | -221.39, -8.51 | -80.75 | -220.1, -5.78 |
| $a_{mealworm}$ | -85.16 | -225.25, -8.54 | -81.83 | -221.3, -5.667 |
| $a_{papaya}$ | -81.60 | -227.12, -6.08 | -80.32 | -226.3, -5.68 |
| $\beta_{eat}$ | -0.40 | -0.94, 0.01 | - | - |
| $\beta_{explore}$ | 0.06 | 0.06, 1.01 | 0.42 | -0.001, 0.09 |
| $\beta_{unsuccessfulfoodtransfer}$ | -0.99 | -0.99, 0.20 | - | - |
| $\beta_{scrounging}$ | -0.39 | -0.39, 0.97 | - | - |
| $\beta_{successfulfoodtransfer}$ | 0.05 | 0.05, 0.76 | 0.15 | -0.06, 0.36 |
| $\beta_{observation}$ | -0.22 | -0.22, 0.004 | - | - |

#### 5.4.2.3 Backward and forward stepwise model selection

The following two stepwise selection methods are called backward stepwise model selection and forward stepwise model selection. These optimise the models through a "greedy" search, where one parameter at a time is dropped (backward) or added (forward), if it creates the best improvement in the WAIC. Results of the backward stepwise selection are presented in Table 5.C.1, and those of the forward stepwise selection are presented in Table 5.C.2, both in the Appendix 5.C, and summarised in Figure 5.9 and 5.10. Figure 5.9 shows the pathway to the backward stepwise model selection method and Figure 5.10 shows the pathway to the forward stepwise model selection method.

From the backward stepwise model selection, the best model seems to be the one with both *unsuccessful food transfer* (UFT) and *explore* as a $\beta$ parameters, however, the model with only *explore*, the model with only *unsuccessful food transfer*, and the model with *unsuccessful food transfer*, *explore* and *successful food transfer* as $\beta$ parameters have very similar WAICs to the model which has both *unsuccessful food transfer* and *explore* as $\beta$ parameters (Fig. 5.9, Appendix Table 5.C.1).

From the forward stepwise model selection, the best model seems to be the one with only *unsuccessful food transfer* as a $\beta$ parameter, however, the model with only *explore*, the model with both *unsuccessful food transfer* and *explore*, and the model with *unsuccessful food transfer*, *explore* and *successful food transfer* as $\beta$ parameters also have very similar WAICs to the model which has only *unsuccessful food transfer* as a $\beta$ parameter (Fig. 5.10, Appendix Table 5.C.2). Both methods do however give similar patterns, and the full results of the four models mentioned above both in the backward and forward stepwise model selection are shown in Table 5.38, where we can see that the values for the $\beta$ for *explore* and *successful food transfers* are positive, while the value for *unsuccessful food transfers* is negative.

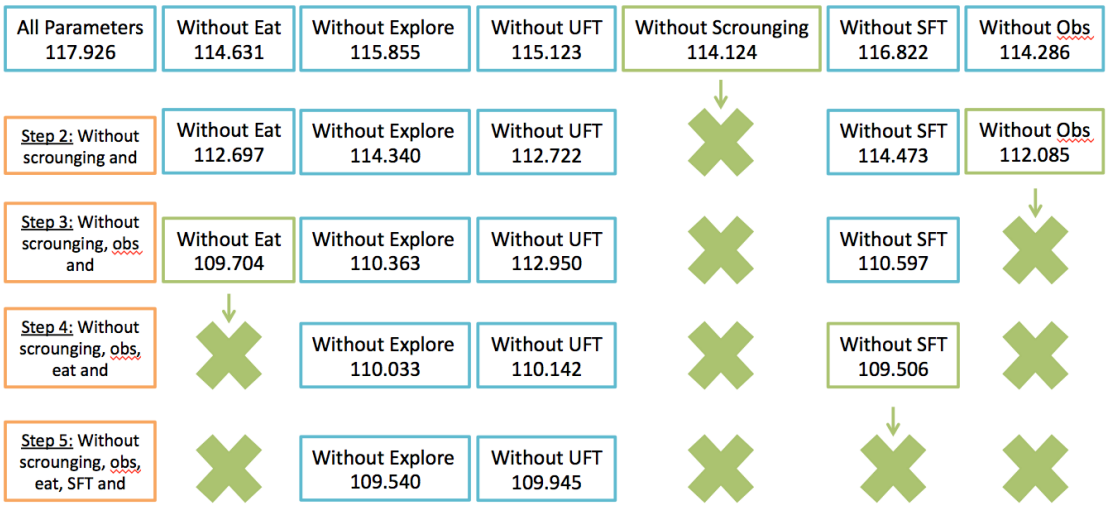


Figure 5.9: Pathway to the backward stepwise model selections, and WAIC of each model. Orange boxes summarise the models at each step. Blue boxes represent the models and their WAIC, while green boxes are the best fitting models at each step

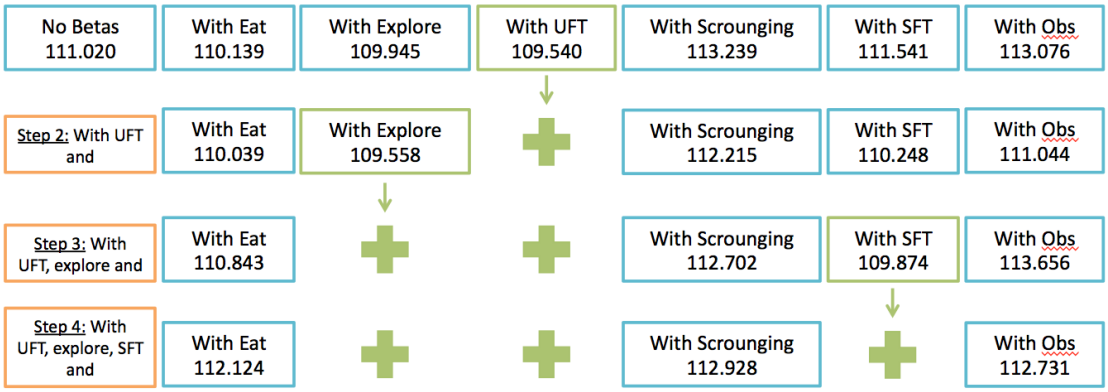


Figure 5.10: Pathway to the forward stepwise model selections, and WAIC of each model. Orange boxes summarise the models at each step. Blue boxes represent the models and their WAIC, while green boxes are the best fitting models at each step

Table 5.38: Model fit results from the backward and forward stepwise model selection. Green cells show parameters for which the 95% credible interval does not overlap with zero

| Parameters/ Stats | Model Fit Results (only UFT) | 95% Credible Interval | Model Fit Results (only Explore) | 95% Credible Interval | Model Fit Results (both UFT and Explore) | 95% Credible Interval | Model Fit Results (UFT, Explore and SFT) | 95% Credible Interval |
|---|---|---|---|---|---|---|---|---|
| WAIC | 109.54 | | 109.95 | | 109.51 | | 109.70 | |
| LP | -53.66 | | -54.10 | | -53.06 | | -52.67 | |
| P_WAIC | 4.96 | | 4.49 | | 6.02 | | 6.79 | |
| PARS | 7 | | 7 | | 8 | | 9 | |
| $a_{apple}$ | -2.99 | -5.07, -1.46 | -2.56 | -4.34, -1.12 | -3.05 | -5.00, -1.52 | -2.93 | -4.95, -1.39 |
| $a_{grape}$ | -0.79 | -1.85, 0.21 | -0.44 | -1.33, 0.38 | -1.08 | -2.19, -0.01 | -0.80 | -1.99, 0.35 |
| $a_{pear}$ | -1.95 | -3.51, -0.55 | -0.51 | -1.43, 0.35 | -1.51 | -3.07, -0.16 | -1.06 | -2.70, 0.45 |
| $a_{cricket}$ | -82.78 | -227.3, -7.48 | -82.92 | -215.7, -6.64 | -85.22 | -232.4, -7.37 | -80.84 | -215.6, -6.57 |
| $a_{mealworm}$ | -82.20 | -224.8, -7.57 | -83.81 | -225.0, -6.11 | -81.84 | -229.3, -6.94 | -82.28 | -229.3, -7.33 |
| $a_{papaya}$ | -85.09 | -232.2, -7.43 | -80.56 | -219.6, -5.45 | -81.98 | -231.3, -7.31 | -82.56 | -231.0, -6.36 |
| $\beta_{explore}$ | - | - | 0.04 | -0.001, 0.09 | 0.04 | -0.01, 0.09 | 0.04 | -0.01, 0.09 |
| $\beta_{UFT}$ | -0.45 | -0.93, -0.03 | - | - | -0.43 | -0.93, 0.01 | -0.41 | -0.89, 0.02 |
| $\beta_{SFT}$ | - | - | - | - | - | - | 0.15 | -0.07, 0.36 |

#### 5.4.2.4 Stepwise model selection based on posterior distribution

The last model selection method is based on uncertainty (width of the posterior distribution), where the model is reduced stepwise to simplify the model by dropping the most uncertain parameter each time, based on the largest 95% credible interval. When all the parameters are included, the $\beta$ with the highest uncertainty in the posterior distribution was the *scrounging* parameter, so the next model includes all parameters except that one. The next most uncertain parameter based on the posterior distribution was *unsuccessful food transfers*, followed by *eating* events, *successful food transfers* and *exploration*. However, the best fitting model was the one that includes parameters for *exploration*, *successful food transfers* and *observations* (Table 5.39). In this model both *exploration* and *successful food transfers* had a positive effect on the probability of choosing a food item, similar to the full model and the models emerging from the forward and backward stepwise model selection. *Observation* had a negative effect on the probability of choosing a food item. This could be

linked to depletion or competition for resources such that if juveniles observed other individuals eat a food type they were more likely to choose another one, or because juveniles had different preferences to other group members, or had different access to food sources.

Table 5.39: Model fit results of stepwise analysis based on the uncertainty of the $\beta$ parameters' posterior distribution. Green cells show parameters for which the 95% credible interval does not overlap with zero

| Parameters/ Stats | Model Fit Results (Without Scrounging) | 95% Credible Interval | Model Fit Results (Without Scrounging and UFT) | 95% Credible Interval | Model Fit Results (Without Scrounging, UFT and Eat) | 95% Credible Interval |
|---|---|---|---|---|---|---|
| WAIC | 114.14 | | 112.09 | | 109.00 | |
| LP | -51.86 | | -52.36 | | -52.35 | |
| P_WAIC | 11.33 | | 8.97 | | 6.64 | |
| PARS | 11 | | 10 | | 9 | |
| $a_{apple}$ | -4.28 | -7.86, -1.79 | -3.41 | -6.44, -1.21 | -2.35 | -4.26, -0.84 |
| $a_{grape}$ | -1.43 | -3.00, 0.11 | -0.57 | -1.67, 0.51 | -0.31 | -1.25, 0.61 |
| $a_{pear}$ | -0.44 | -2.37, 1.36 | 0.05 | -1.52, 1.68 | -0.55 | -1.82, 0.62 |
| $a_{cricket}$ | -81.66 | -229.03, -7.79 | -83.35 | -221.68, -6.91 | -79.13 | -214.69, -6.59 |
| $a_{mealworm}$ | -82.59 | -224.69, -7.56 | -79.52 | -217.39, -6.16 | -81.15 | -225.48, -6.25 |
| $a_{papaya}$ | -81.78 | -232.93, -6.15 | -82.09 | -226.43, -5.51 | -82.60 | -227.04, -5.96 |
| $\beta_{eat}$ | -0.36 | -0.85, 0.04 | -0.21 | -0.59, 0.10 | - | - |
| $\beta_{explore}$ | 0.41 | 0.03, 0.89 | 0.29 | -0.02, 0.67 | 0.09 | 0.03, 0.15 |
| $\beta_{UFT}$ | -0.45 | -1.03, 0.10 | - | - | - | - |
| $\beta_{scrounging}$ | - | - | - | - | - | - |
| $\beta_{SFT}$ | 0.32 | 0.12, 0.65 | 0.36 | 0.08, 0.68 | 0.29 | 0.03, 0.55 |
| $\beta_{observation}$ | -0.06 | -0.12, 0.01 | -0.07 | -0.13, -0.12 | -0.05 | -0.09, -0.001 |

| Parameters/ Stats | Model Fit Results (Without scrounging, UFT, eat, and SFT) | 95% Credible Interval | Model Fit Results (Without scrounging, UFT, eat, SFT, and explore) | 95% Credible Interval |
|---|---|---|---|---|
| WAIC | 111.49 | | 112.98 | |
| LP | -54.23 | | -55.70 | |
| P_WAIC | 5.67 | | 4.35 | |
| PARS | 8 | | 7 | |
| $a_{apple}$ | -2.65 | -4.53, -1.27 | -2.51 | -4.35, -1.04 |
| $a_{grape}$ | -0.63 | -1.57, 0.28 | -0.03 | -0.72, 0.68 |
| $a_{pear}$ | -0.87 | -2.07, 0.23 | -0.65 | -1.72, 0.40 |
| $a_{cricket}$ | -83.78 | -228.0, -6.73 | -81.56 | -227.28, -6.07 |
| $a_{mealworm}$ | -82.45 | -224.9, -6.55 | -81.68 | -233.93, -5.55 |
| $a_{papaya}$ | -83.90 | -238.7, -6.23 | -81.04 | -222.37, -5.92 |
| $\beta_{eat}$ | - | - | - | - |
| $\beta_{explore}$ | 0.06 | 0.004, 0.12 | - | - |
| $\beta_{UFT}$ | - | - | - | - |
| $\beta_{scrounging}$ | - | - | - | - |
| $\beta_{SFT}$ | - | - | - | - |
| $\beta_{observation}$ | -0.02 | -0.06, 0.02 | 0.01 | -0.02, 0.04 |

From all of the four methods (hypothesis testing, “straddle” method, backward and forward stepwise selection, and stepwise selection based on posterior distribution), the best fitting model was the one containing $\beta$s for the *explore*, *successful food transfers* and *observation* parameters. When dropping one of those three parameters at time (Table 5.40), we can determine which parameter has the most impact on the fit. Here, the $\beta$ for the *explore* parameter seemed to be the most important in making the model fit the data, since the model without it had the worse fit, followed by the $\beta$ for *successful food transfers* and the $\beta$ for *observation* parameters.

Table 5.40: Model fit results of subsets of the best fitting model

| Parameters/Stats | Model Fit Results (with Explore, SFT and Observation) | Model Fit Results (with SFT and Observation) | Model Fit Results (with Explore and Observation) | Model Fit Results (with Explore and SFT) |
|---|---|---|---|---|
| WAIC | 109.00 | 113.61 | 111.49 | 110.35 |
| LP | -52.35 | -55.40 | -54.23 | -53.64 |
| P_WAIC | 6.64 | 5.47 | 5.67 | 5.58 |
| PARS | 9 | 8 | 8 | 8 |

As mentioned earlier, with the best fitting model, I obtained a positive effect of *exploration* and *successful food transfer* events on the juveniles' choices in the testing phase, but a negative effect of *observation*. There were however also some strong correlations between several parameters which means it is difficult to determine, with certainty, which social experience(s) is key in driving future preferences (see Fig. 5.11). In order to further understand the relationship between the three parameters in the best fitting model, I looked at the individual patterns for the dependent variable and the predictor variables of that model. Figures 5.12 to 5.18 show the data for the juveniles' eating choices in the second phase, and *explore*, *successful food transfer* and *observation* events in the first phase for juveniles AF3T12, AF3T4, AFT3, AloneT2, BO2T2, BO2T3 and SuperT1 respectively.

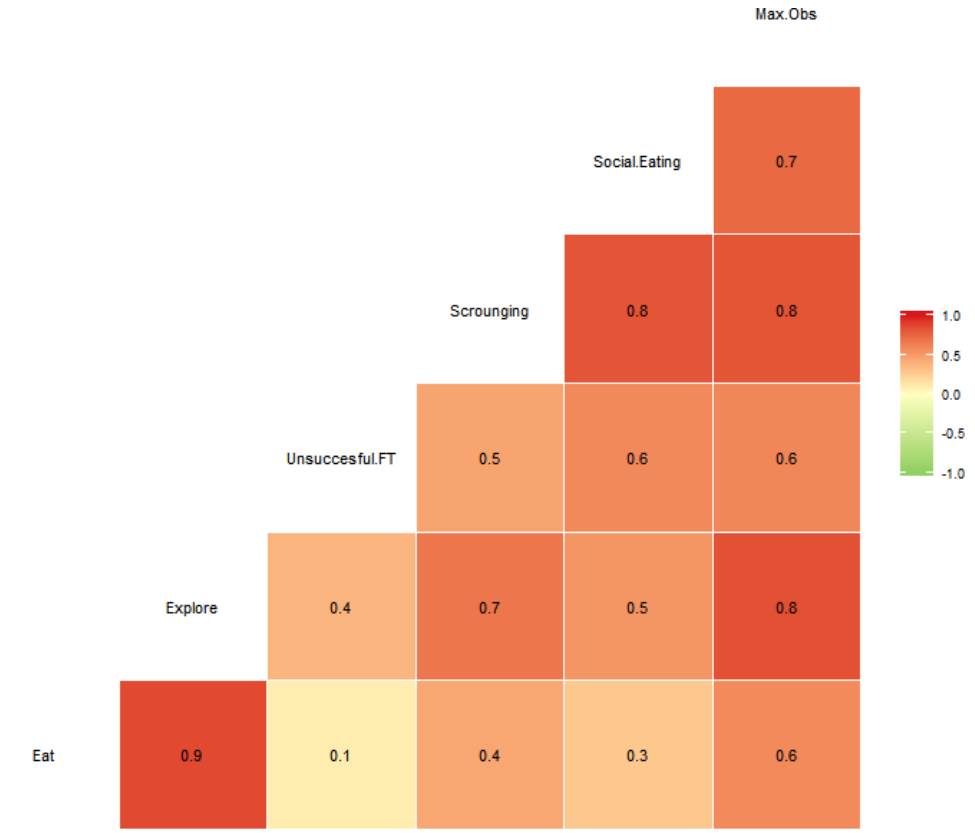


Figure 5.11: Correlation matrix of the parameters representing the previous experience of juveniles. "Social eating" corresponds to successful food transfers

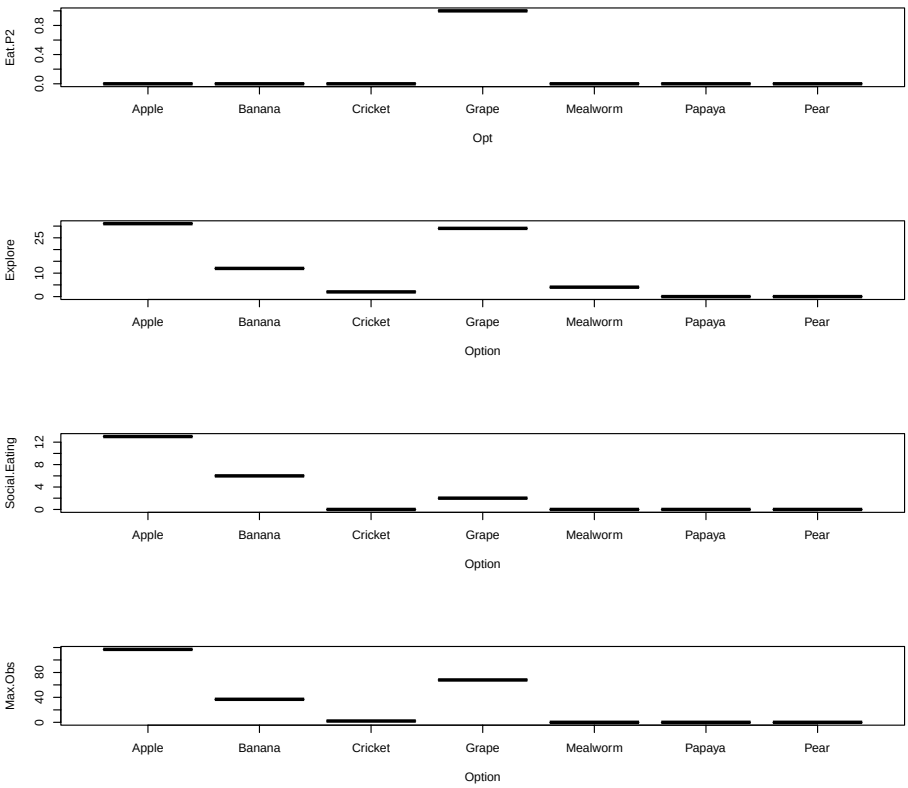


Figure 5.12: Number of (1) *eating* events in the second phase, (2) *explore*, (3) *successful food transfer* and (4) *observation* events in the first phase, for each food type, for juvenile AF3T12. "Social eating" corresponds to successful food transfers

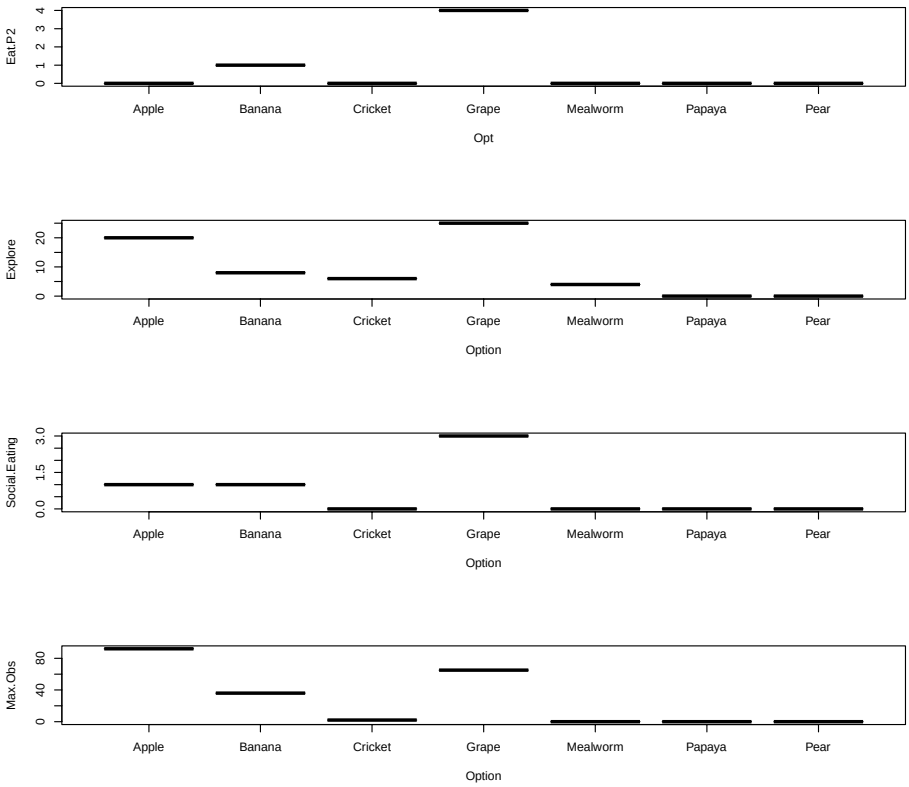


Figure 5.13: Number of (1) *eating* events in the second phase, (2) *explore*, (3) *successful food transfer* and (4) *observation* events in the first phase, for each food type, for juvenile AF3T4. "Social eating" corresponds to successful food transfers

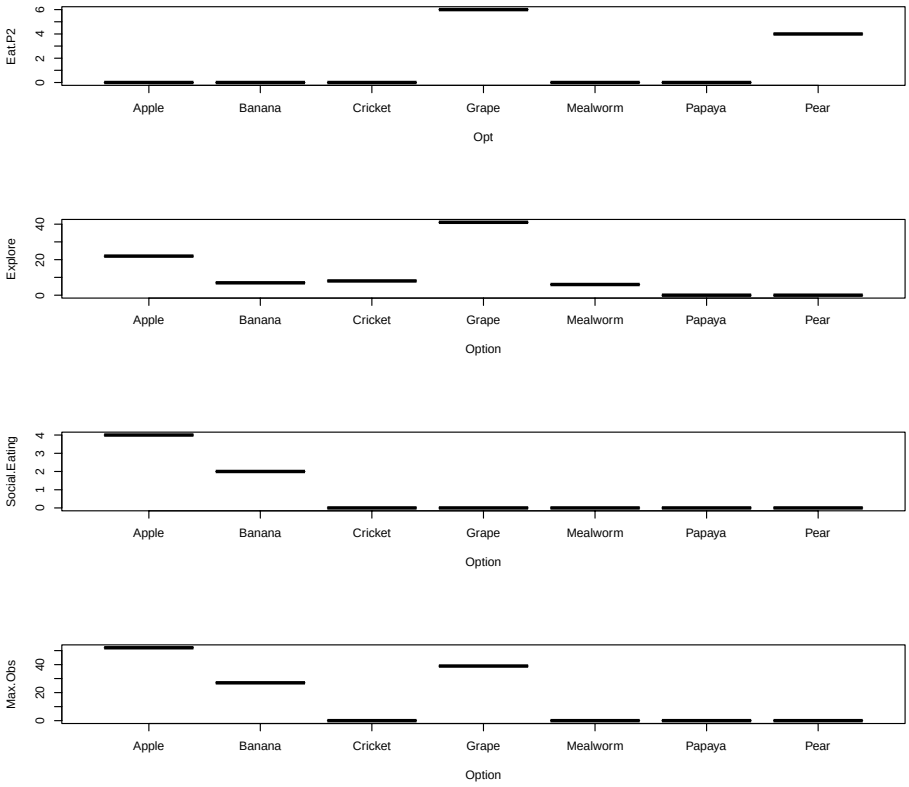


Figure 5.14: Number of (1) *eating* events in the second phase, (2) *explore*, (3) *successful food transfer* and (4) *observation* events in the first phase, for each food type, for juvenile AFT3. "Social eating" corresponds to successful food transfers

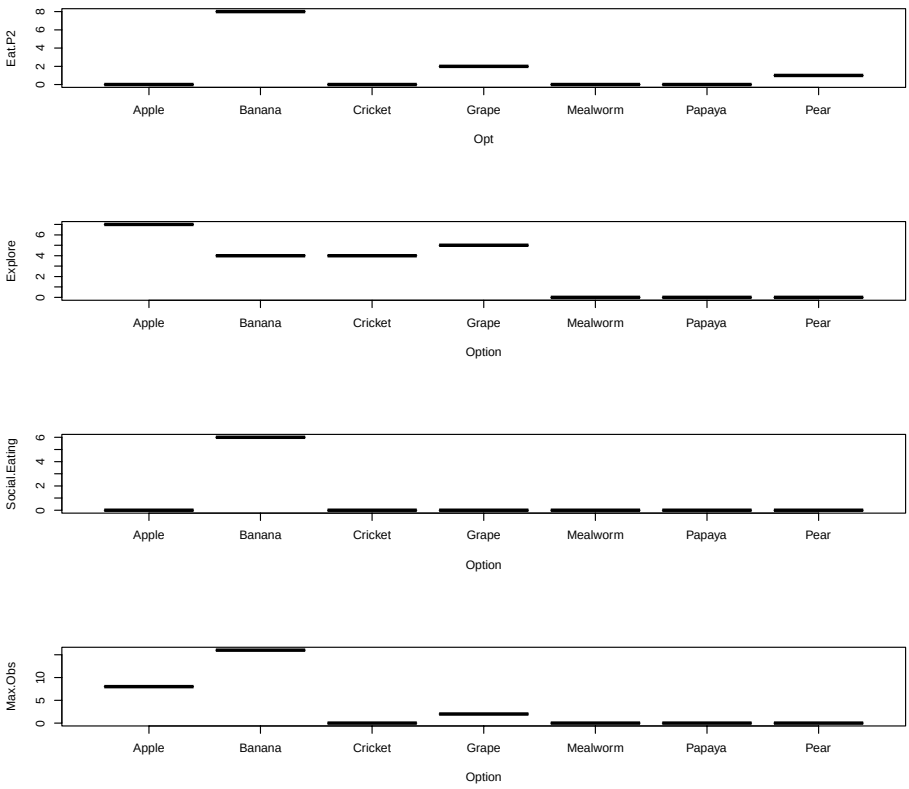


Figure 5.15: Number of (1) *eating* events in the second phase, (2) *explore*, (3) *successful food transfer* and (4) *observation* events in the first phase, for each food type, for juvenile AloneT2. "Social eating" corresponds to successful food transfers

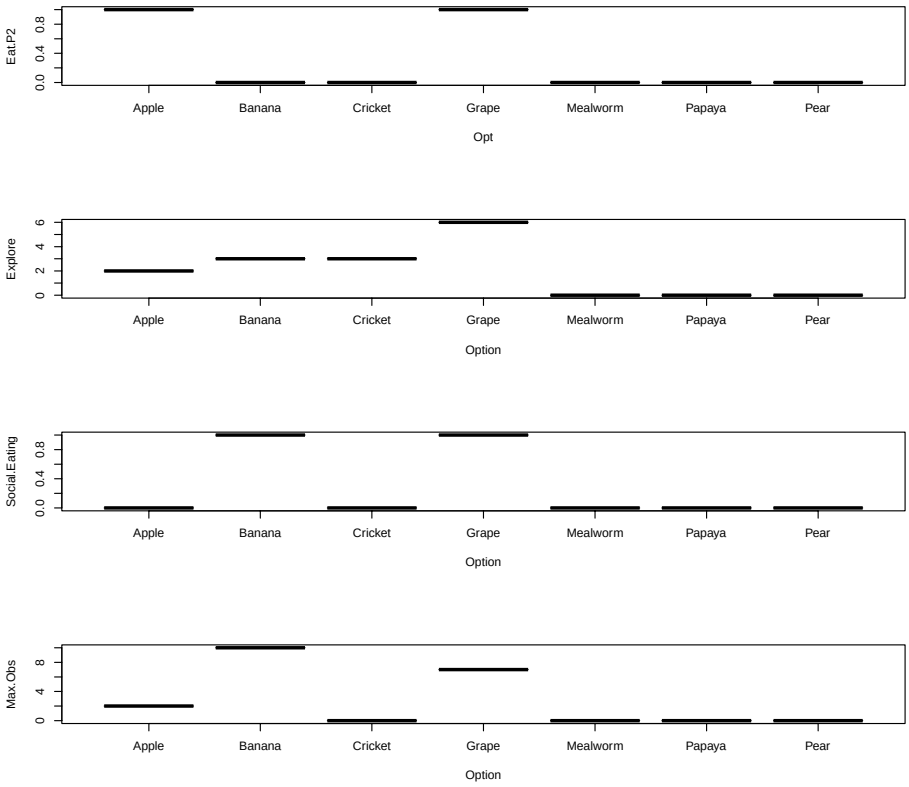


Figure 5.16: Number of (1) *eating* events in the second phase, (2) *explore*, (3) *successful food transfer* and (4) *observation* events in the first phase, for each food type, for juvenile BO2T2. "Social eating" corresponds to successful food transfers

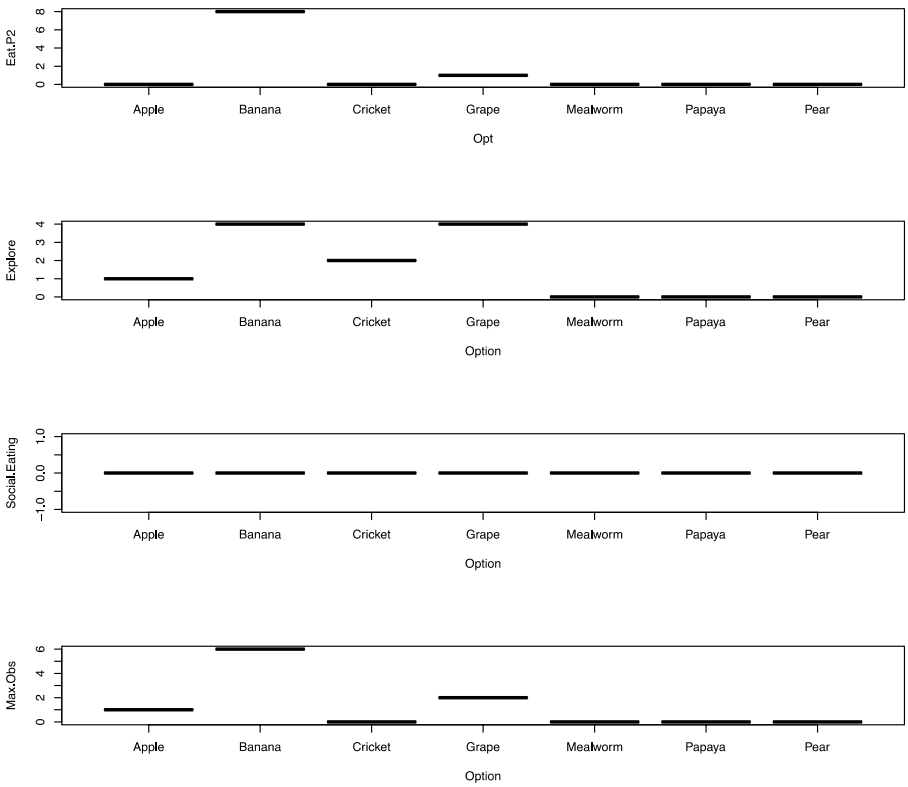


Figure 5.17: Number of (1) *eating* events in the second phase, (2) *explore*, (3) *successful food transfer* and (4) *observation* events in the first phase, for each food type, for juvenile BO2T3. "Social eating" corresponds to successful food transfers

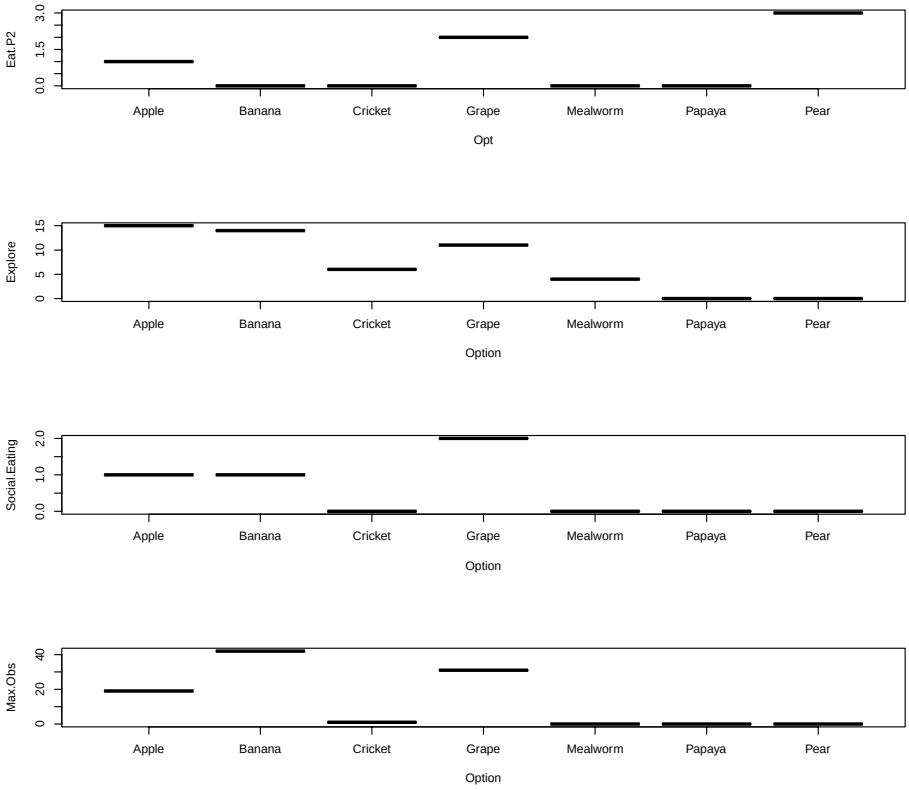


Figure 5.18: Number of (1) *eating* events in the second phase, (2) *explore*, (3) *successful food transfer* and (4) *observation* events in the first phase, for each food type, for juvenile SuperT1. "Social eating" corresponds to successful food transfers

When only having *exploration* and *successful food transfers* as predictors in the model, without *observation*, the WAIC was higher than the best fitting model. When having only the predictor for *observation* events in the model, the $\beta$ value was positive but overlaps with zero. This suggested that *observation* could have a potential compensatory effect on *exploration* and *successful food transfer*, where *observation* regulates the positive effects of *exploration* and *successful food transfers*. This compensatory effect of the *observation* parameter could explain the negative value of its $\beta$ in the best fitting model, but a positive value of its $\beta$ in the model that only contained observation as a predictor.

In fact, when we look at the juveniles' foraging patterns, including only the parameters from the best fitting model, the patterns for *exploration* events always predicted fairly well the eating choices in the first trial of the second phase. *Successful food transfer* was very good at predicting juvenile choices but only for some juveniles. Moreover, the *observation* parameter seemed to compensate for the other previous-experience variables. For instance, for the first three individuals (Fig. 5.12, 5.13 and 5.14) apple was observed a lot, but was not a popular feeding choice amongst those juveniles. A negative value for the beta corresponding to the observation parameter would mean that the choice for this food type would decrease highly. However, if a food type was not observed a lot, such as banana for those three juveniles, then a negative value of *observation* would have a lesser effect in decreasing the probability of that food type being chosen.

### 5.4.3 Summary of results in relation to food transfers

Table 5.41: Summary of the results

| | |
|---|---|
| 1st Criterion: Modification of behaviour | There is little evidence showing that novel foods were transferred more successfully than familiar food. However, transfers were more successful when the donor had at least one previous ingestion of that specific food type.<br>Juveniles did not attempt to obtain novel food more than familiar food, and they were as successful in obtaining novel food compared to familiar food once they were engaged in a transfer and the adults were resisting. However, they were more successful in obtaining food that they had ingested at least once.<br>Adults resisted as much during transfers of novel food as they did during transfers of familiar food.<br>When analysing patterns of food transfers for juveniles in the second phase, the sample size was too small for results to be conclusive, but again, food familiarity seemed to have little effect on predicting the success of a food transfer. |
| 3rd Criterion: Learning | Food transfers seemed to have an effect on the juveniles' future foraging decisions. The more a juvenile had successfully obtained a food type from another individual in the first phase, the more likely it was to choose this food type in the first trial of the second phase of the experiment. Individual exploration was also positively correlated with future food choices.<br>Unsuccessful food transfer had a negative effect on juveniles' choices, suggesting that it might lead juveniles to avoid the food types not transferred. |

## 5.5 Discussion

The aim of this study was first to examine whether, as Rapaport (1999) suggests, adult GLTs modify their behaviour in transferring more novel food versus familiar food to juveniles. The second goal was to analyse whether juvenile GLTs could learn about appropriate diet from food transfers. This would test two criteria of the hypothesis that GLTs exhibit teaching.

### 5.5.1 Findings

#### 5.5.1.1 Probability of succeeding in a food transfer

There was weak evidence that juveniles are more likely to succeed in obtaining food from a transfer than are non-juveniles (receiver age is the best

predictor). This supports the idea that in this species, food transfers are not primarily used for reciprocity or coercion, but for the development of the young (be it nutritional provisioning or learning purposes). However, there was little evidence that novel foods were more successfully transferred than familiar ones, suggesting that donors do not modify their behaviour in this way. This does not support Rapaport's (1999) theory and Lefebvre's (1985) findings that food transfers are used to teach juveniles what foods are good to eat. Food transfers could therefore play an important role in provisioning the young.

It was also found that whether the donor had previously ingested a type of food or not, was a very good predictor of the probability of succeeding in a food transfer. This shows that the donor needs to be familiar (ingested at least once) with the food type before transferring it successfully. The donor first needs to know that the food is palatable before transferring it, or be familiar with the experimental set up. This supports the important role of the donor in the transfer. On the other hand, the recipient's previous success is not an important factor in predicting the success of a food transfer. This suggests that recipients are involved in transfers with all types of food, regardless of whether they ingested a particular food type before or not.

Figure 5.3 shows the proportion of successful food transferred according to the donor's ingestion experience and food familiarity, as discussed above. When I uses *receiver success* and *donor success* >1 in the model instead of >0, the importance of *donor success* dropped from 100% to 49% (effect size = 0.27; 95% C.I. = -0.49, 1.03) which suggests that the first feeding event of the donor is important. The donor might only need to experience the food and set up of the experiment once before it gives the food away. Thus, individual learning and habituation might be necessary before engaging in any social interactions. Thornton and Raihani (2010) suggest that evidence of teaching about novel food would be strengthened by evidence that donors are willing to incur the cost of sampling novel food before transferring it to receivers, to assess the food's palatability. The fact that transfers are more successful when the donor has sampled the food option at least once, suggest that potential donors need to

sample the novel food to make sure it is palatable, before transferring it. Novel food types that have been ingested by the donor once in our experiment could be compared to prior-adult sampled food in Rapaport's (1999) experiment, which finds that both prior-adult sampled foods and novel foods are transferred more than familiar food. However, when analysing the food transfers in the second phase, the food familiarity (familiar, prior-adult sampled or novel) does not seem to impact the probability of success of a food transfer, particularly when juveniles are receivers and non-juveniles donors. This could be due to more fine-grained transfer preferences, where particular food types rather than food familiarity are transferred preferentially. For instance, there seems to be a strong bias against transferring papaya.

Furthermore, in the second phase, the new juveniles were also shown to be 0.18 times as likely to receive food from other individuals successfully as were non-juveniles. This could be explained by several reasons. First, the juveniles in the second phase were approximately seven months old, which is two months older than the juveniles in the first phase. Fewer food transfers usually occur at that age, and adults might have considered those juveniles to already be proficient at obtaining food on their own, and thus not have preferentially transferred novel or prior-adult sampled food items. This would reflect that if GLT teach their young, they are not necessarily sensitive to the level of skills of their young, or their previous experience, but might use a proxy such as age as was found in meerkats (Thornton & McAuliffe, 2006). On the other hand, the fact that juveniles are less successful in receiving food items could be because non-juveniles are still invested in providing the older juveniles, and that those four younger juveniles are just a subset of the individuals that group members are attempting to provide for. If the older juveniles (the ones that were juveniles in the first phase) were also included in the analysis, a different pattern might have emerged.

In previous studies it was found that fathers were more involved in food transfers than other group members. By looking at the interactions between age and sex (no genetic data were available to assess paternity), it seems that in this

species the adult males did not transfer food more successfully than other group members, since the relative importance of the interaction in the model is very low. There was however some evidence for an effect of sex in the probability of succeeding in food transfers (*receiver sex* was the best predictor). When transfers from non-juveniles to juveniles were selected, female receivers were less likely to obtain food from a food transfer successfully, compared to males. It is possible that the sexes have different maturation periods, in which case food transfers might be particularly directed towards one sex at a specific time of development. However this is unlikely as the species is not sexually dimorphic (K. Brown & Mack, 1978). Differential investment in offspring could also potentially be linked to the sex of dispersal if one sex dispersed earlier than the other. In fact, if males dispersed prior to females to new groups, females would have a longer time period to learn what food to forage from in their natal range. Because food transfers can be costly, donors might preferentially transfer to males if females have more time to learn from passive social learning or asocial learning if they spend more time in the natal group.

#### 5.5.1.2 Probability of attempting a food transfer and probability of succeeding with a transfer given resistance

When investigating the probability of juveniles attempting a food transfer, it was found that food familiarity did not affect juveniles' attempts to obtain food from other individuals. If information, as well as nutritional values, is transferred from non-juveniles to juveniles during transfers of novel food, then juveniles are not active in requesting that information, since they attempt to get familiar food from non-juveniles as much as they attempt to get novel food. This is supported by the earlier findings that the recipients' previous experience with the food is not important in predicting the probability of success of a food transfer (5.4.1.2). Transfer patterns are therefore due to the adults' active modification of behaviour, and not due to the juveniles' attempts.

Although juveniles attempted transfers of novel food as much as those of familiar food, they attempted more food transfers of a food option that they had

previously ingested in the context of this experiment, since the *receiver's previous success* with a food option (as a binary variable) was an important predictor in determining the probability of attempting to obtain that food option. Juveniles were more likely to attempt a food transfer of a food that they have had at least one prior interaction with. This could suggest that the juveniles require some short adaptation time to the experimental set up before engaging in social interactions such as food transfer, or that there are some short terms effects of the familiarity of the food, as seen with the *receiver success*, but no long term effects on their probability of attempting a food transfer, as seen with the *food familiarity* variable.

When analysing the probability of success of a transfer given that there was resistance in the transfer, no effect of the *receiver age* was observed. Moreover, when selecting transfers with resistance between non-juveniles and juveniles, no effect of *food familiarity* was revealed. This further supports the hypothesis that juveniles are not attempting to obtain novel food more than familiar food, and thus that any patterns of transfers observed are determined by the donor, not the receiver.

#### 5.5.1.3 Probability of resistance (during a transfer)

When investigating the probability of resistance in a transfer between non-juveniles and juveniles, it was found that donors were as likely to resist attempted food transfers when the food was novel as when it was familiar. Similar findings were found when looking at the *donors' previous success* (both as continuous and binary): donors were as likely to resist attempted food transfers when they had had previous ingestion experience with the food option compared to when they had not. Those results suggest that donors attempt to keep familiar food as much as they attempt to keep novel food. Thus non-juveniles do not use food transfers as a way to get rid of novel foods, which could have explained the pattern observed.

However, one limitation of the analysis could be that measuring resistance is a crude estimate of adult's motivation to keep a food item. In fact, it only measured the presence or absence of resistance during a transfer, and not the amount, duration, or whether the donor stopped resisting during the transfer before the juvenile obtained the food item. If those aspects of resistance were taken into account, a different pattern of results might have been observed.

Overall, results from the analysis of the food transfers suggest that GLTs transfer more novel compared to familiar food to their juveniles, although not statistically significantly more. However this pattern is not explained by juvenile attempts to get more novel food, even when already engaged in a transfer, or that adults attempt to keep more familiar food. Food transfers are however more likely to be successful if the donor has had prior experience with that particular food type. What remains to be shown is whether juveniles acquire knowledge from those food transfers.

#### 5.5.1.4 Predicting juvenile choices in the second phase based on their previous experience

From the different model comparison methods a general pattern emerged: previous exploring and successful food transfers events repeatedly came out as being good predictors of the foraging choice of a juvenile in the second phase of the experiment. Moreover, there was often an additional negative social effect, which could either be driven by unsuccessful food transfers or observations. However, the negative value of the observation parameter could have been an artefact of the model to increase the fit rather than a representation of the effect of those previous experiences. Unsuccessful food transfers can be a good predictor on its own in some models, suggesting that its role is not purely compensatory. In fact, the negative effect of unsuccessful food transfers where the recipient did not receive food could be indicative of the donor preventing the recipient from obtaining the food because that food might not be as palatable, which would lead the recipient to avoid that food type after unsuccessful food transfers. Combined with the findings that successful food transfers were a

relatively good predictor, tentative conclusions can be drawn of the importance of earlier food transfers as a whole to juveniles' subsequent foraging decisions.

#### 5.5.1.5 Limitations on the analysis of the effects of food transfers on juvenile foraging decisions

One limitation of this study, which is similar to the one in Chapter 6, is the low sample size. This is particularly relevant for the analysis of the foraging choices of juveniles, because the probability of choices was made based on one trial, which were very little data. Hence it is hard to draw definite conclusions from the data set. However, especially for the Bayesian model framework, those results are still important in consolidating the priors for future experiments on this topic.

There are several other limitations to the Bayesian models that could explain the patterns observed. For instance, the models do not take into account the temporal evolution of the predictors during the training phase. Later observations in the first phase could be more important than earlier ones. In these experiments bananas were the main food being eaten at the start, before all the other fruits were sampled to the same extent. Because the model takes the cumulative value of all food being eaten, bananas end up being eaten more overall, even if apples or grapes are eaten more at the end of the first phase. With the cumulative effect, there are more bananas than grapes being observed to be eaten. However, five of the seven juveniles ate more grapes than bananas in the first trial of the second phase. If there were different weights given to observations of what other individuals eat based on recency, or if only later observations were taken into account in the model, then observation could have a positive effect. In fact, when observation is the only parameter included corresponding to previous experience, then it has a positive effect.

There are factors other than recency that could be affecting juveniles choices in the testing phase that are not accounted for in the model, such as satiation, monopolisation or competition, depletion, and preferences for novel

foods. There is also the possibility that the previous experience parameters are non-linear (in the model they are currently fit in a linear fashion). For instance, linearity implies that there are no saturation or recency effects. However, if the parameters were included in a non-linear way, this would expand the number of parameters in the model, which could be a problem leading to over fitting given the small size of the data. The models used are quite coarse-grained, as the data used collapsed all previous events of the first phase rather than allowing individuals' attractions to be updated after each foraging event. Using this data could affect the suitability of the various predictor used.

Another limitation could be the similarity between pears and apples. In fact, for two individuals, a lot of pears are eaten in the first trial of the second phase, compared to their previous experience with it (none). In the second phase of the experiment, pears were picked up often, but usually immediately dropped after individuals took a bite from them. From observing the individuals it looked like the tamarins were mistaking pears for apple, and realising the mistake once they took a bite. If pears were indeed mistaken for apples, this could explain why two juveniles ate a lot of pears without having any previous experience with them, but having quite high experience with apples.

With the different methods, I did not obtain the same best fitting model, probably due to the high correlations between predictor variables. Despite all the limitations, the best model that was obtained included effects of exploration, successful food transfers and observation. Based on this we can draw the tentative conclusion that successful food transfers seem to play a role in the foraging knowledge acquisition of juveniles. Moreover, as mentioned earlier, it seems that unsuccessful food transfers are used to provide information about food to be avoided. Taking those results together suggests that juveniles learn from food transfers what food is good to eat and what food to avoid. Food transfers could direct the juveniles' decisions towards palatable food and away from unpalatable ones. We can also tentatively draw the conclusion that juveniles are quite neophilic, since exploration seems to play an important role in the juveniles' foraging choices. However there are still some uncertainties

about the model and parameters, since depending on the approach I get different best models, and depending on the combination of parameters used I get different effects of each parameter. This will lead to follow up research and models that do take the various factors mentioned into account. In a Bayesian framework, the present results can also be used as future priors: we can use the present best model as a prediction for future research when more data are available.

### 5.5.2 General points

#### 5.5.2.1 Future work

Future work could include investigating the food transfer rates towards juveniles of different age. In captivity, Hoage (1982) has found that at 16 weeks, juveniles still receive 90% of their food from food transfers, and in the wild, Ruiz-Miranda et al. (1999) report that the rate of food transfers from non-juveniles to juveniles does not drop drastically until the juveniles are 9 months old. In our experiment, juveniles were slightly older than in Hoage's (1982) experiment, but within the range of juveniles in Rapaport's (1999) experiment. Despite this, it would be informative to investigate whether the type of food transferred is constant across ages of juveniles, or if there is a specific period in the development of the juveniles where adults transfer more of one type of food than another (for instance highly nutritional food in early infancy to insure the survival of the offspring, or foods that are difficult to process or rare later in the infancy to increase the diet breadth of the juveniles before they become independent). Rapaport (1999) notes that the exact function of food transfers (teaching versus provisioning versus both) could depend on the age of the recipient. If different food types were transferred at different periods of development, this could explain the seemingly contradictory results found in Rapaport (1999), where juveniles were between 13-37 weeks old and adults were found to transfer more novel food than familiar food, and Price and Feistner (1993), where juveniles were between 7-21 weeks old and adults were not found to transfer more novel food than familiar food. Rapaport (1999) suggests that food transfers might be mainly used as a nutritional benefit for

younger individuals [as in Price and Feistner's (1993) study] and might be used for further teaching purposes or to transmit information on top of nutrients in older individuals [as shown by Rapaport's (1999) findings] that have survived the earlier months of life. The juveniles in our study were closer to the age of the ones studied by Rapaport's (1999), but a wider range of ages in juveniles would give a clearer picture of the use of food transfers in this species.

It would also be interesting to examine whether food transfers at a particular period in the development of the juveniles have more of an impact on the juveniles' future foraging decisions than transfers at other times in the development, i.e. is there a critical period for learning what food is good to eat. Schiel and Huber (2006) found that juvenile common marmosets change their social bias at specific phases of the development. A similar developmental change could be happening in juvenile GLTs, thus transfers occurring at a particular time of the development could have more impact in the subsequent foraging decisions than transfers occurring at other times.

Similarly, it would be interesting to investigate whether food transfers from particular individuals have more of an impact on the juveniles' future foraging decisions, than food transfers from other individuals. For instance vervet monkeys (*Chlorocebus aethiops*) copy more from dominant females compared to dominant males (van de Waal, Renevey, Favre, & Bshary, 2010) and infants adopt the option demonstrated by the mother more than that demonstrated from other individuals (van de Waal, Borgeaud, & Whiten, 2013; van de Waal, Krützen, Hula, Goudet, & Bshary, 2012). In chimpanzees "moss-sponging" spreads through social networks (Hobaiter, Poisot, Zuberbuhler, Hoppitt, & Gruber, 2014) and Horner et al. (2010) claim that chimpanzees preferentially copy individuals with a previous record of success of introducing novel behaviour into the group. In our experiment, we found no effect of a specific role of adult males, but juveniles could create bonds with particular individuals, regardless of their sex or age, which could have a greater influence on the juveniles' development (Laland, 2004).

Because active transfers from adults to juveniles are more likely to involve vertebrate or invertebrate prey (Ruiz-Miranda et al., 1999), future work should involve prey items to which GLTs are attracted. Dehydrated mealworms and crickets were used in this experiment because they were highly preferred food for captive populations in previous studies (E. C. Price & Feistner, 2001; Rapaport, 1999). However they were highly avoided by all individuals in the wild, potentially because of their smell or inertness. It would be interesting to include in future studies live or frozen prey rather than dehydrated ones, to see if GLTs still avoid them. If not, it could be examined whether prey are transferred to the same degree as fruits. However, although some research mentions high rates of food transfers in GLTs (Ruiz-Miranda et al., 1999), Miller and Dietz (2005) found a fairly low rate of prey transfers in wild GLTs (<6% of prey items ingested), which is closer to the rate of food transfers found in this study. Hence transfer patterns of insects might not be too different from the results obtained in this study.

Moreover, the different novel and familiar foods were not counterbalanced in the first and second phase. This introduces a confound between the novelty of a food, and a general preference for or palatability preference for specific items. This can be seen, for instance, with lower ingestion rates for papaya. Two novel fruits and two novel insects were used, so that a range of novel food would help disentangle preference from novelty. Although food items were chosen for this study based on preferences in captive studies, and based on seasonal availability, other strategies could have been used to prevent this confound. One option would have been to introduce the apple and grape in the first phase, and papaya and pear in the second phase, to half of the groups, as was done in this experiment, and then the other half of the groups would have access to papaya and pear in the first phase and apples and grapes in the second phase, to counterbalance for food specificity. A second option would have been to use the same familiar food in each pot, in order to control for food palatability and nutritional differences, but dye the food in different colours, as was done for the hen experiment in Chapter 7.

All food transfer studies in the wild in *Leontopithecus* species have been done with GLTs. Not much is known of the natural pattern of transfers in the three other *Leontopithecus* species. All three species have relatively similar habitats and social organisation. It would therefore be interesting to investigate whether transfers are used similarly in all *Leontopithecus* species.

#### 5.5.2.2 Literature

In this experiment, food transfers were found to be predominantly successful when they were from adults to juveniles. This is in accordance with previous findings (Ruiz-Miranda et al., 1999), and further supports the uniqueness of food transfers in the Callitrichid family (G. R. Brown et al., 2004; Feistner & McGrew, 1989). However, from this experiment, it is still difficult to disentangle the *nutritional* hypothesis from the *information donation* hypothesis concerning the roles of food transfers in GLTs. The pattern of transfers suggests that novel foods might be transferred more than familiar ones, but food familiarity was not found to be an important predictor in the success of food transfers. Moreover, food transfers are seemingly important in predicting the choices of juveniles when they forage independently. More data on food transfers spanning a wider variety of food types, including foods that are difficult to handle, and spanning a wider age range of juveniles, are necessary to disentangle the two hypotheses, and get a clearer understanding of the role of donors in the transfers and the role of food transfers in the juveniles' foraging choices.

From analysing the effects that previous experience had on juveniles' foraging decisions, it was found that food transfers seem to have a stimulus enhancement effect, since juveniles are attracted specifically to the food type manipulated by the donor if that item was then transferred to them, and would avoid choosing that food type if it was not transferred. Moreover, we also found a strong effect of exploration on the juveniles' decisions. Visalberghi et al. (2003) found that individual experience is sufficient in determining food preferences in captive tufted capuchins (*Sapajus apella*). This experiment has findings that

support their conclusion for GLTs, but also shows that ingestion is not necessary for the juveniles to form preferences. The GLTs' exploratory behaviour could however have been directed by social facilitation or local enhancement, if individuals witnessed a lot of other individuals in their group near particular food types even if not necessarily foraging on them.

In conclusion, it seems that food transfers can be used to provision the young, for the direct nutritional benefit, but also may contribute to the juvenile learning to forage (Ruiz-Miranda et al., 1999) since food transfers seem to be a good predictor of juveniles' foraging decisions. However, the findings in this experiment are not consistent with the teaching hypothesis. Juveniles therefore seem to learn foraging preference from food transfers, without the transfers being actively modified to promote learning. This experiment suggests that, donors do seem to assess food palatability prior to transfers, regardless of their novelty.

# Chapter 6:

# Role of food-offering calls in wild golden lion tamarins: evidence for teaching behaviour?

## 6.1 Abstract

This chapter examines whether the role of food-offering calls in wild golden lion tamarins (GLTs) is to teach juveniles the quality of foraging substrates. I introduced a novel substrate and manipulated the rate of food-offering calls by introducing playbacks in some groups. The playbacks allowed me to mimic a putative teaching scenario in this species. I then compared the foraging behaviour of juveniles in groups that were exposed to the novel substrate in addition to the playbacks to the foraging behaviour of juveniles in groups that were exposed to the novel substrate without playback calls. I found that food-offering calls had immediate effects on the number of times juveniles interacted with the novel substrate, the number of times they inserted their hand in the substrate and the number of times they ate food from the substrate, as well as a long-term effect on their eating behaviour. Those findings are consistent with teaching in golden lion tamarins through stimulus enhancement.

## 6.2 Introduction

In GLTs, in addition to food transfers, there is another behaviour that potentially fulfils Caro & Hauser's (1992) criteria for teaching behaviour: food-offering calls. Food-offering calls are an important part of GLT's repertoire, and are a variant of food calls, which are high-pitched chattering vocalisations with a peak frequency of about 5 kHz, also called clucks. Food calls are usually emitted when an individual sees, or possesses, food (K. Brown & Mack, 1978). If the cluck sound is produced on its own in the presence of food ("food call") then the animal clucking is usually not approached by listeners (Boinski et al., 1994). But if the individual emits variable tonal sounds following the clucks ("food-offering call") then another individual usually approaches the individual emitting this vocalisation and takes food without much resistance from the original possessor (K. Brown & Mack, 1978; Ruiz-Miranda et al., 1999). This chapter will investigate the additional role of food-offering calls in indicating the type of location of a food source.

### 6.2.1 Vocalisations

Because of the dense habitat in which they live, vocalisation is the most efficient communication mode for GLTs, particularly for activities such as maintaining group cohesion, warning about predators or advertising food sources. However, few studies have been conducted on vocal communication in GLTs, and evenwer on scent and visual communication (review by Ruiz-Miranda & Kleiman, 2002). Most of the vocalisation studies in callitrichids date back to the 1990's to early 2000, with a few from the mid 1970's. Very little research has been conducted on this topic in the last decade. However, previous captive and wild studies have shown that GLTs have various vocalisation types that are used in specific contexts, in association with particular behavioural patterns. For instance, variations of "cluck" calls can be used in a foraging context or an aggression context, while multi-syllable "long calls" are used for group cohesion, and "trill-rasp" are predominantly used by juveniles for begging (Boinski et al., 1994; Ruiz-Miranda et al., 1999).

### 6.2.2 Food calls

Food calls are found in various primate species, and can be emitted as an arousal reaction to the presence of food or emitted to indicate the presence of food to conspecifics (Fedurek & Slocombe, 2013; Slocombe & Zuberbühler, 2007). Encouraging neighbours to remain in the proximity of the calling individual, as was found in chimpanzees (Fedurek & Slocombe, 2013), could decrease food theft from non-group members, as in ravens (Heinrich & Marzluff, 1991) or increase group level vigilance while foraging (Elgar, 1986). There can also be an "audience effect" where individuals behave differently according to who is in the vicinity. For instance, in red-bellied tamarins (*Saguinus labiatus*) (Caine, Addington, & Windfelder, 1995) and cotton-top tamarins (*Saguinus oedipus*) (Elowson, Tannenbaum, & Snowdon, 1991), individuals increase their food call rates when visual contact with group mates is obstructed. Audience effects are also found in captive GLTs where individuals vocalise more when they are alone with an unfamiliar individual, than when both their mate and an

unfamiliar individual are present (Inglett, French, & Dethlefs, 1990). In this social context, the food calls could potentially recruit groupmates to the food source (Caine et al., 1995). In GLTs, food calls are emitted in the context of finding food or communicating about foraging, and are not necessarily always associated with food transfers. Similarly, in the rest of the primate lineage, calls emitted in the presence of food are not necessarily associated with food transfers. This is especially the case if no infants or juveniles are involved (Hauser, 1992; Hauser, Teixidor, Fields, & Flaherty, 1993).

### 6.2.3 Food calls in golden lion tamarins

In the previous chapter, GLTs were shown to transfer food to other individuals, and such transfers often take the form of unresisted food-stealing, where the individual with the food does not resist the stealing. What makes food exchange in GLTs distinguishable from other forms of unresisted food stealing observed in primates, is the presence of "invitational" signals preceding the transfer (K. Brown & Mack, 1978). Of those signals, Brown and Mack (1978) found that food calls (they do not distinguish food calls from food-offering calls in this paper) seemed to be the most significant in predicting an unresisted food transfer. In captivity, 78% of food transfers were preceded by some signalling from the individual with the food item (eye contact, food call, offering position and approach) and 90% of the successful food transfers were preceded by a signal (K. Brown & Mack, 1978). Ruiz-Miranda et al. (1999) found that 11% of food transfers were preceded by a food-offering call. In this context, GLT calls emitted in a foraging context might plausibly transmit information about the state of the individual: whether they are likely to share food with juveniles, or not. The difference in percentage of food transfers preceded by signals in the two studies could be explained by the fact that Brown and Mack (1978) do not differentiate between food calls and food-offering calls, while Ruiz-Miranda et al. (1999) only focus on food-offering calls.

Food call emissions have been shown to vary with context in GLTs. Benz et al. (1992) found that in captivity GLTs increase their rate of food calling based on

the extent to which they prefer a particular food: the rate of calling increases for preferred food. Similar findings are reported in birds (Marler et al., 1986a). Given that GLTs are known to use different vocalisation in response to terrestrial and aerial predators (M. I. Castro et al., 1998; Ruiz-Miranda pers. obs) and that they are a species for which the diet can consist of over 80 plant species, and many species of invertebrate and vertebrate prey (Dietz et al., 1997; Lima, Farias, & Farag, 1995), it would be unsurprising if they had evolved signals to classify food. Although calls emitted in the Benz et al. (1992) experiment do not provide external information about particular foods (which is not expected given that their diet consists of a wide variety of food), they have the potential to transmit information about the individual's preference, and experience, with that food, on top of transmitting information about the individual. Other callitrichids, such as the red-bellied tamarins, have also been found to increase their food call rate with the magnitude of their preference for the food (Caine et al., 1995).

Food calls are a broad category of calls that signal the preference of an item or that foraging is taking place. Within this category, there is the special case of food-offering calls, which are used in one context only: signalling the willingness to share a food item. More recently, Rapaport and Ruiz-Miranda (2002) examined the role of food-offering calls from a new angle. Instead of indicating the willingness of an individual to share its food item, or the individual's dietary preference, Rapaport and Ruiz-Miranda (2002) suggested that the food-offering calls could also be used by adults to indicate the type of location of a source of food. This is particularly interesting if the juveniles, for whom those calls are emitted, can learn about those foraging locations, and use the information acquired later in life. There is evidence from comparison of vocalisation of captive, reintroduced, and wild-born GLTs that the vocal structure could be learned (although there is no direct evidence that this is the case) (Ruiz-Miranda, Archer, & Kleiman, 2002). Whether GLTs learn information about their environment from vocalisations is, however, still unknown.

### 6.2.4 Evidence of food-offering calls as teaching in golden lion tamarins

In the wild, Rapaport and Ruiz-Miranda (2002, p. 1064) found three instances where "*wild adult golden lion tamarins appear to have directed their immature offspring to a location where a hidden prey item was located*", and Rapaport (2011) reports a further twelve instances of this behaviour. Seemingly adult GLTs modify the context in which food-offering calls are used. This, according to the authors, corresponds to Caro and Hauser's (1992) first criterion of the teaching definition. However, whether the juveniles learn from this modified behaviour remains untested. In the observations reported by Rapaport and Ruiz-Miranda (2002) and Rapaport (2011), adults were foraging without any visible prey, and emitted calls that attracted juveniles to the foraging place. The juvenile then started foraging at this location and retrieved the prey. In turn, the emitter made no attempt to obtain the prey (Rapaport & Ruiz-Miranda, 2002). Although the substrate in which the prey were foraged varied (crevices in vines, knotholes in branches, broken branch tips, curled dead leaves, tangle of dead leaves and vines), the prey always were concealed within vegetation (Rapaport, 2011). This behaviour is similar to co-foraging (where a juvenile approaches and forages on a substrate where another individual is foraging, and where no food-offering calls had been emitted), but co-foraging without a call being emitted by the adult was relatively unsuccessful: only 3.33% (n=13 juveniles; range: 0-8.9%) of "*juvenile-initiated social foraging bouts"* resulted in *"successful prey capture*" (Rapaport, 2011, p. 748; Rapaport & Ruiz-Miranda, 2002). Adults therefore seemingly emit a call to attract a juvenile to a location where they have found a prey but not retrieved it.

Giving calls to alert group members to the presence of food is widespread among mammals and birds, however, using a food-offering call to indicate their willingness to transfer food is less common. Even more rare is switching context in which to use a call, from food-transfer to location indication. As per Caro and Hauser's (1992) teaching definition, the adults modify their behaviour by emitting this food-offering call in the recruitment context. Only juveniles were found to respond, but it is not known whether the emitters behave similarly

when there are no juveniles in the group (Rapaport & Ruiz-Miranda, 2002). Moreover, it can be said that the behaviour is costly, because not only does the emitter not retrieve the prey, but there is also a risk of the juvenile losing it, which might force the emitter to retrieve the prey and replace it in the substrate. The cost criterion has however never been directly investigated in this context. Moreover, there still are no data examining whether juveniles learn the properties of substrate on which to find prey from foraging following those calls.

Food-offering calls are part of the (allo-)parental behaviour of GLTs and are emitted only in the presence of juveniles (Feistner & Price, 1991; Joyce & Snowdon, 2007; Rapaport, 2011; Rapaport & Brown, 2008). Moreover, Rapaport and Ruiz-Miranda (2002) found that this change in context in which they are emitted was observed mainly when the juveniles were between 31-36 weeks old. This is the age at which the juveniles have had initial success at foraging prey on their own, but have not yet mastered the skill. The twelve juveniles observed by Rapaport (2011) were found in a wider age range: 20-45 weeks, but two thirds of this behaviour occurred after the juveniles were 32 weeks old. Adults might therefore modify their behaviour in order to facilitate successful foraging in juveniles. Rapaport (2011) further suggested that the calls might be used in a different context according to the age or developmental stage of the juveniles. In fact, the food transfer rate drops as independent success increases in juveniles. The juveniles' food acquisition strategy switches from mainly relying on food transfers to foraging independently between 21-32 and 33-44 weeks (Rapaport, 2011). Rapaport suggests that as the juveniles get older, food-offering calls are used less in a food-transfer context, because juveniles are foraging independently more often, and instead adults start using them to direct the juveniles' attention to a substrate in which they can successfully retrieve prey independently (Rapaport, 2011). Adults seemingly start using food-offering calls in this new context when the juveniles increase their independent foraging efforts, but before their prey-capture rates increase - when they are still learning about foraging skills and techniques. It is because of the timing of the change in the use of the calls that Rapaport (2011) suggests that the adults seemingly teach, or offer information, to their young on which substrate they can

successfully find prey. In fact, nearly half of the food transfers occur on the substrate on which the prey is found (Ruiz-Miranda et al., 1999). This supports the hypothesis that adults donate food related information to their young by providing them with an opportunity to learn about the substrate on which prey items can be found. Thus similar to the potential transfer of information through food transfers, food-offering calls constitute a candidate case of teaching behaviour in GLTs. In captivity, there are data from two studies that support the idea of adult-directed foraging assistance, called scaffolding in Humle and Snowdon (2008). Humle and Snowdon (2008) and Dell'Mour et al. (2009) both had experimental studies where knowledgeable adult callitrichids encouraged young to solve a novel foraging task, which is similar to obtaining food from a novel substrate successfully.

### 6.2.5 Aim of this experiment

Rapaport (2011) suggests that to determine the role of food-offering calls, and whether they fulfil Caro and Hauser's (1992) third criterion for teaching, an experimental set up supplementing calls with a playback at a novel substrate would determine whether juveniles find food more efficiently or earlier in life as a direct effect of the calls. That is the aim of the experiment described in this chapter. The experiment investigated whether juvenile GLTs can learn to associate played back food-offering calls with a foraging substrate, and whether those juveniles that received the playback food-offering calls are subsequently more likely to forage on that substrate, and to do so more efficiently, when independent, than the juveniles that did not receive playback calls. This allowed me to answer the main question as to whether juveniles learn about the substrate on which they find food through food-offering calls. The experiment has two goals:

1. **To discover whether juvenile GLTs are more likely to interact with a novel foraging substrate and whether they would forage more efficiently (insert their hands and eat) when the food-offering call rate is increased through playbacks (immediate effect), than when the food-offering call is left at its natural rate.**

2. **To assess whether juveniles, once they have reached independence, are more likely to forage from a previously novel substrate, more efficiently, if they have associated it with food-offering calls when they were younger, compared to juveniles that were exposed to the novel foraging substrate without playbacks of food-offering calls (long-term effect).**

GLTs are opportunistic omnivores (Goldizen, 1987), as a consequence of which Benz et al. (1992) did not expect GLTs to elicit food calls for particular foods, but rather for particular classes of foods such as fruits, vegetables, prey etc. Similarly, because GLTs eat a variety of food items that vary in location by season, I predicted that juveniles would learn to forage on the novel substrate (substrate type) rather than learn where to forage (location). Moreover, because GLTs' food sources can be depleted easily, I expected individuals to generalise from a previous productive food site to another (Rapaport, 2011). Therefore, if the playbacks are effective I expected either an increase in foraging success, or an increase in effort on that or a similar substrate, in GLTs previously exposed to playbacks compared to juveniles that did not experience playbacks.

## 6.3 Methodology

### 6.3.1 Design

This experiment compares the performance of wild juvenile GLTs in an experimental condition in which juveniles are introduced to a novel substrate while exposed to playbacks of food-offering calls, to the performance of juveniles in the control condition, where they are exposed to the novel substrate without the presence of food-offering playbacks (normal rate). The performance of juveniles in the two conditions are compared both at the time of exposure (immediate effects: training), and six months later (long-term effects: testing).

### 6.3.2 Subjects

The same GLT subjects in the food transfer experiment in Chapter 5 were studied here. This experiment followed the experiment in Chapter 5. At the start of the experiment all juveniles were between 20.5 and 26 weeks old. Group POR2 was unreachable for this experiment and left out. Group AF2 had lost its juveniles. Although the experiment included group AF2, the analysis does not. Only the juveniles present in the two phases of the experiment were included in the analysis (N= 7 juveniles; N= 35 individuals in total in the five groups). Two groups had two juveniles, and the remaining three groups had one juvenile each.

### 6.3.3 Apparatus

The novel substrate was a cubic plastic box painted brown on all sides except the top and door sides (Fig. 6.1). Because of its availability, the box is similar to that used with vervet monkeys (van de Waal, Claidière, & Whiten, 2015, 2013). However it was modified so that there was only one option to open the door: sliding it. The box was either attached to a foraging platform or to branches at human chest level. The door side could slide open with a handle. It was kept open 1.4 cm across, to allow for a narrow opening, and was held in place with magnets. The strength of the magnets was enough to prevent the subjects from sliding the door open, except in two trials. The box was filled with slices of bananas (1 to 1.5 bananas were used in each trial), and a slice of banana was placed on top of the box to attract the subjects to the box. Bananas are familiar and highly desirable food to those habituated groups, and are offered to them when researchers attempt to capture individuals. The opening of the box was wide enough for the subjects to insert their hand into and retrieve food items. The apparatus was designed such that extracting food from it resembled a behaviour that GLTs perform naturally in the wild when they have to extract prey from narrow holes or cavities, but doing so from a novel substrate.

For playbacks, a Saul Mineroff (SME-AFS) speaker and an iPod mini were used to emit the sounds. The main energy of the calls was between 5-10 kHz, and

we used a 5-Watt speaker, with a frequency response from 100 Hz to 12 kHz. The speaker was placed under or behind the box and the amplitude of the sounds emitted by the playback calls was around 70 dB, which is in the auditory range of decibel level for GLTs (Ruiz-Miranda et al., 2002; Sabatini & Ruiz-Miranda, 2008). Food-offering calls were taken from prior work on GLT vocalisations in the population, and were from adults that were unknown to the juveniles. Three adult calls were used for each of the three groups in the experimental condition. One of the calls is shown in Chapter 2, Figure 2.3. A call was looped ten times to create a long enough stimulus, which lasted between five and eight seconds.

Figure 6.1: Box used for the novel foraging substrate experiment

### 6.3.4 Procedure

As in the food transfer experiment in Chapter 5, this experiment took place over two time periods: the first phase provided the opportunity for the juveniles to associate the playback calls with the novel foraging box (training phase), and the second phase allowed me to assess the juveniles' learning in the longer term (testing phase).

#### 6.3.4.1 Training

The training phase of the experiment took place from February to March 2014. The five groups were assigned to two treatment categories: 2 x control groups and 3 x experimental groups. In the control condition, groups were exposed to a novel foraging substrate. In the experimental condition, on top of being exposed to a novel foraging substrate, food-offering calls were played back to the subjects at irregular intervals when they were in the vicinity of the box, from speakers placed under the foraging box. Calls were played back when any member of the group was in my visual field. This included individuals approaching, and individuals interacting with the box. Most of the time the entire group was present in the vicinity of the box.

Similar to the food transfer experiment in Chapter 5, the box (and playbacks in the experimental condition) was presented to the subjects over five trials. Trials were not considered valid if there was no interaction with the box or if two or fewer individuals (of any age) were present on the foraging platform for less than 85 seconds in total, and if the group taking part in the trial was displaced or was displacing another group from a different condition (see Table 6.A.1 in the Appendix for a list of valid trials). Trials were repeated until five valid trials had been completed per group, and all trials were filmed for later analysis. Trials continued until all the individuals had left (average length of trial: 9 min 36 secs).

#### 6.3.4.2 Testing

The testing phase of the experiment took place in September 2014. For the "testing phase", five trials were conducted for each group deploying the same criteria as in the training phase (see Table 6.A.2 in the Appendix). This time, however, all groups only had access to the box containing food (i.e. no groups were subject to playbacks) as the aim was to see if the earlier playbacks had any long-term effects, especially on the juveniles.

### 6.3.5 Video analysis

As in the previous experiment, videos were watched using the software package VLC. During playback the behaviours (Table 6.1) were recorded as states, but treated in the analysis as events. 10% of the data were double coded and the inter-observer reliability was found to be high ($r=0.80$, $p<2.2e-16$ for all behaviour; interaction: $r=0.85$, $p=5.42e-12$; insertion: $r=0.74$, $p=1.42e-7$; eating: $r=0.90$, $p=2.16e-14$) (R Development Core Team, 2015).

Table 6.1: Definitions of the dependent variables

| Behaviour | Definition |
|---|---|
| Presence around the box | The individual is in the camera frame, where the box is at the centre. |
| Interaction | The individual shows interest in the box by orientating its face towards the box and being close enough to sniff it (no physical contact, but close proximity) or handle the box (requires physical contact with parts of the box). The different areas of the box that were interacted with were also recorded: top, back, sides, door, and bottom. |
| Insertion | A hand (or head in some cases) is inserted in the box to retrieve bananas – can be successful (bananas extracted) or not. |
| Eating | After being extracted the food item was ingested. Only one eating event was counted for each food extraction. |

Other foraging behaviour such as scrounging, food transfers, and eating transferred food, as defined in the previous experiment, were also recorded. Behaviours were recorded on Microsoft Excel. The time and duration of those events were also logged, and additional individuals with which they interacted (in case of food transfers) were also noted.

### 6.3.6 Statistical analysis

Learning was inferred from the number of successful eating events, and eating events were compared across conditions to examine the role of food-offering calls in the learning process. Two factors determine the number of successful eating events: 1) the number of insertion events, and 2) the probability that insertion successfully retrieves food. I therefore first analysed

those two determining factors before testing for an overall effect of playbacks on 3) the number of eating events. I also looked at how specific the potential effects of the food-offering calls are by investigating more general effects such as 4) attracting individuals' attention towards the box (interaction events), and comparing with the more specific effect of encouraging insertion of the hand. Finally, I examined (5) the change in all three behaviour patterns (interaction, insertion and eating) across trials, particularly in the testing phase.

Any behavioural difference between the conditions could be due to an immediate effect of the playbacks (e.g. calls could make the substrate more attractive), or to a long-lasting behavioural difference that persists into the testing phase of the experiment. The analysis is therefore broken down into the training phase (to investigate any potential immediate effect of playbacks), and the testing phase (to look at long-lasting effects). The influence of playbacks on the difference of behavioural events between the training and testing phase is also examined.

To determine what variables influenced eating behaviour I also analysed the probability of insertion events leading to a successful eating event (which is the number of successful eating events out of the total number of insertions for each individual in each stage of the experiment). This is different from analysing the number of eating events, because it looks at variables affecting the probability of an eating event, given that the juvenile has already inserted its hand in the box. It can therefore be considered as a measure of persistence in obtaining food. This was modelled using a GLM with a binomial error structure and logit link function (D. Bates et al., 2015). The main effects are the training and testing phase as well as whether or not there was playback in the training phase (condition). A second GLM was used to analyse the data, with phase and condition as main effects, and it also included an interaction between the phase and the condition. This was done to obtain models comparable to the randomisation tests, where we could look for an effect of individual learning through the phase and an effect of social enhancement through the condition. Pairwise comparisons of phase x condition

combinations were then used to break down the effect of the interaction using GLMs.

Regarding the changes of all three behaviours (interaction, insertion and eating) across trials, a post-hoc analysis was conducted to compare the first three trials of the second phase (henceforth referred to as "phase 2.1"), to the last two (or three when there were a total of six trials) trials (henceforth referred to as "phase 2.2"), to test whether there was an initial difference in behaviour between the conditions that disappeared due to a lack of reinforcement. The number of events for each behaviour was averaged over both conditions, and a randomisation test was used as explained previously. This allows me to examine the effect of the playbacks on a more fine-grained temporal spectrum.

## 6.4 Results

### 6.4.1 Insertion behaviour

#### 6.4.1.1 Training phase (1)

During the training phase, on average, juveniles in the control group inserted their hands into the novel box less (M = 4.33, SE = 4.33) than juveniles in the experimental condition (M = 37.00, SE = 13.29). There was suggestive evidence of a difference (t(3.61) = 2.34, p = 0.087; see Fig. 6.2, A); and it did represent a large-sized effect (r= .776, 95% C.I. = -0.16, 0.93).

#### 6.4.1.2 Testing phase (2)

During the testing phase, on average, juveniles in the control condition inserted their hands into the novel box less (M = 33.33, SE = 8.57) than juveniles in the experimental condition (M = 58.50, SE = 11.02). This difference was not significant (t(4.99)= 1.80, p = 0.143; see Fig. 6.2, B). However, it was estimated to be a large-sized effect with r = .628 (95% C.I. = -0.22, 0.87).

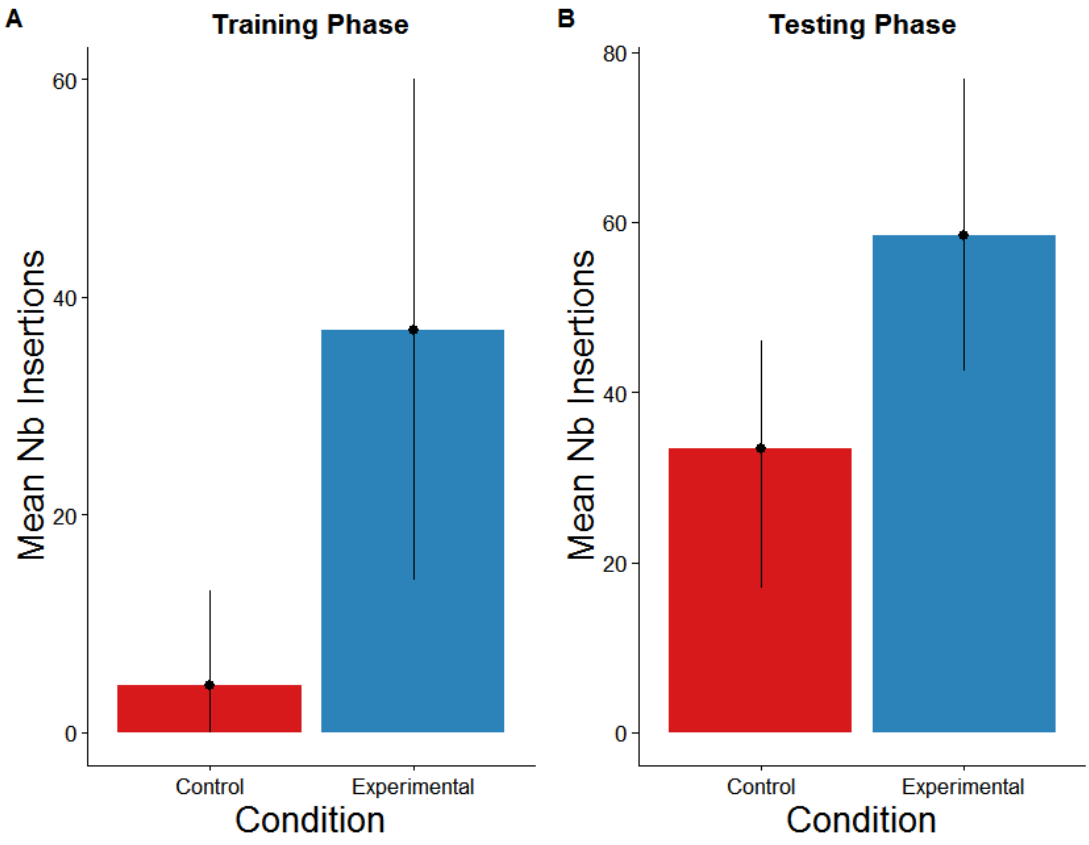


Figure 6.2: Mean number of insertion events in juveniles, per condition. Error bars are the 95% C.I. (not assuming normality)

6.4.1.3 Difference

The influence of playbacks on the difference in numbers of insertion events between the training and testing phase was also examined. In most cases individuals increased their insertion and eating behaviour from the training to the testing phase (Table 6.2, Table 6.8). I therefore wanted to know if the increase between the two phases differend betweem the two conditions, as the number of insertion events in the testing phase could be influenced by those in the training phase.

Table 6.2: Raw data about juveniles' insertion behaviour

| Juveniles | Sex | Condition | Insertion Training Phase | Insertion Testing Phase | Total Insertion | Difference between Training and Testing Phase |
|---|---|---|---|---|---|---|
| AFT3 | F | Ctl | 13 | 46 | 59 | 33 |
| AF3T12 | M | Exp | 59 | 45 | 104 | -14 |
| AF3T4 | F | Exp | 61 | 40 | 101 | -21 |
| AloneT2 | M | Exp | 13 | 89 | 102 | 76 |
| BO2T2 | M | Ctl | 0 | 17 | 17 | 17 |
| BO2T3 | F | Ctl | 0 | 37 | 37 | 37 |
| SuperT1 | F | Exp | 15 | 60 | 75 | 45 |

On average, juveniles in the control condition increased their insertion behaviour more (M = 29.0, SE = 6.11) than juveniles in the experimental condition (M = 21.5 SE = 23.43). This difference was not significant (t(3.40) = -0.31, p = 0.826) and it did represent a small-sized effect (r = .166, 95% C.I. = -0.78, 0.67).

### 6.4.2 Probability of success of an insertion event

Visual interpretation of the proportion of insertion events that led to eating events (Fig. 6.3), suggested there were more successful insertions leading to eating events in the testing phase of the experiment for those individuals exposed to playback calls in the training phase, suggesting that individuals in this condition might have learned, as they are more efficient.

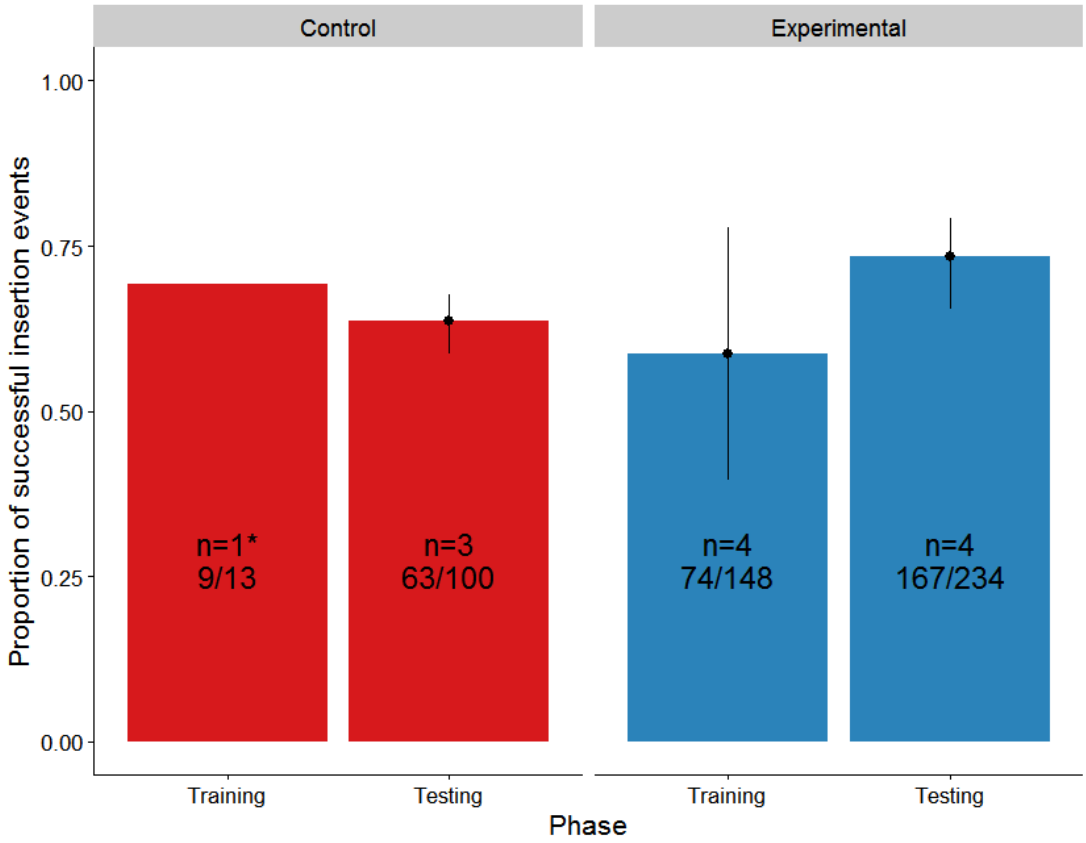


Figure 6.3: Mean proportion of insertion events leading to an eating event in juveniles, per condition per part. Error bars are 95% C.I. (not assuming normality because of proportion). *n* is the number of individual, the numerator is the number of eating events, and the denominator is the number of insertion events. * The first bar has no error bar because, although there are three juveniles in the control condition, only one of them inserted its hand in the novel substrate

The results of the analysis of the probability of insertion events leading to a successful eating event are shown in Table 6.3. The data with an interaction between the phase and the condition were also analysed, and the results are shown in Table 6.4.

Table 6.3: Summary of generalised linear model looking at the proportion of successful insertion events given the phase and the experimental condition

| Predictor | Estimate | Std. Error | 95% C.I. | z value | Pr(>\|z\|) |
|---|---|---|---|---|---|
| Intercept | -0.12 | 0.27 | -0.64, 0.40 | -0.44 | 0.658 |
| **Phase: Testing** | **0.78** | **0.21** | **0.37, 1.18** | **3.79** | **0.0001** *** |
| Condition: Exp | 0.20 | 0.23 | -0.26, 0.65 | 0.84 | 0.401 |

Table 6.4: Summary of generalised linear model looking at the proportion of successful insertion events given the phase and the condition, and their interaction

| Predictor | Estimate | Std. Error | 95% C.I. | z value | Pr(>\|z\|) |
|---|---|---|---|---|---|
| Intercept | 0.81 | 0.90 | -0.95, 2.58 | 1.35 | 0.177 |
| Phase: Testing | -0.28 | 0.64 | -1.53, 0.97 | -0.44 | 0.661 |
| Condition: Exp | -0.81 | 0.62 | -2.03, 0.41 | -1.30 | 0.193 |
| Phase: Condition Exp | 1.19 | 0.67 | -0.13, 2.51 | 1.77 | 0.076 |

In a model assuming additive effects of phase and condition, there was little evidence of an effect of condition but there was strong evidence that there was a higher proportion of successful insertions in the testing phase than the training phase ($z = 3.79$; $p = 0.0001$; Table 6.3). However, this pattern was entirely driven by the data from the experimental condition (see Fig. 6.3). Indeed, when an interaction between condition and phase was included, there was suggestive evidence that the effect was stronger in the experimental group than in the control group ($z = 1.77$; $p = 0.076$; Table 6.4). This increase in success between the training and testing phase only observed in the experimental condition could be a result of a) food-offering calls having a negative effect in the training phase b) food-offering calls having a positive effect in the testing phase 2; or c) both.

To further investigate the effect of the interaction I conducted pairwise comparisons of phase and condition. Tables 6.5, 6.6 and 6.7 show the result of the analysis respectively with the training phase of the control condition, the training phase of the experimental condition and the testing phase of the control condition as the baseline.

Table 6.5: Summary of generalised linear model looking at the proportion of successful insertion events given the new factor combining phase and the condition, with the training phase of the control condition as the baseline

| Predictor | Estimate | Std. Error | 95% C.I. | z value | Pr(>\|z\|) |
|---|---|---|---|---|---|
| Intercept | 0.81 | 0.60 | -0.37, 1.99 | 1.35 | 0.177 |
| Training Phase, Experimental Condition | -0.81 | 0.62 | -2.03, 0.41 | -1.30 | 0.193 |
| Testing Phase, Control Condition | -0.28 | 0.64 | -1.53, 0.97 | -0.44 | 0.661 |
| Testing Phase, Control Condition | 0.10 | 0.62 | -1.11, 1.31 | 0.17 | 0.868 |

Table 6.6: Summary of generalised linear model looking at the proportion of successful insertion events given the new factor combining phase and the condition, with the training phase of the experimental condition as the baseline

| Predictor | Estimate | Std. Error | 95% C.I. | z value | Pr(>\|z\|) |
|---|---|---|---|---|---|
| Intercept | 1.82e-16 | 0.16 | -0.32, 0.32 | 0.00 | 1.000 |
| Training Phase, Control Condition | 0.81 | 0.64 | -0.44, 2.06 | 1.30 | 0.193 |
| **Testing Phase, Control Condition** | **0.53** | **0.26** | **0.01, 1.05** | **2.01** | **0.044 *** |
| **Testing Phase, Experimental Condition** | **0.91** | **0.22** | **0.48, 1.34** | **4.17** | **3.03e-05 ***** |

Table 6.7: Summary of generalised linear model looking at the proportion of successful insertion events given the new factor combining phase and the condition, with the testing phase of the control condition as the baseline

| Predictor | Estimate | Std. Error | 95% C.I. | z value | Pr(>\|z\|) |
|---|---|---|---|---|---|
| Intercept | 0.53 | 0.21 | 0.13, 0.94 | 2.57 | 0.102 * |
| Training Phase, Control Condition | 0.28 | 0.64 | -0.67, 1.53 | 0.44 | 0.661 |
| **Training Phase, Experimental Condition** | **-0.53** | **0.26** | **-1.05, -0.01** | **-2.01** | **0.044 *** |
| Testing Phase, Experimental Condition | 0.38 | 0.25 | -0.11, 0.88 | 1.51 | 0.131 |

From Figure 6.3 it looked like the interaction between phase and condition appeared to be due to a positive effect of the experimental manipulation in the testing phase and a negative effect in the training phase. However this was a misleading pattern because of the lack of data in the training phase of the control condition. Instead pairwise comparison of phase and condition combinations revealed that none of the phase-condition combinations are different from the training phase of the control condition but that is because there were very few data from the training phase of the control condition. It is therefore necessary to focus on the other differences. Table 6.6 shows that both the juveniles in the testing phase of the control and experimental conditions were more successful than juveniles in the training phase of the experimental condition. Table 6.7 also reveals that while juveniles in the testing phase of the experimental condition were not more successful than juveniles in the testing phase of the control condition, juveniles in the testing phase of the control condition were more

successful than juveniles in the training phase of the experimental condition. Hence, although there was weak evidence of an interaction between phase and condition (Table 6.4), this was entirely driven by a difference between the training phase of the experimental condition and the testing phase of the control and experimental conditions, as well as the lack of data in the training phase of the control condition. This is in line with the analysis without the interaction between phase and condition (Table 6.3) that suggested an effect of phase, rather than condition, on the proportion of insertion events that lead to an eating event (a measure of persistence). Figure 6.4 summarises the pairwise comparison findings.

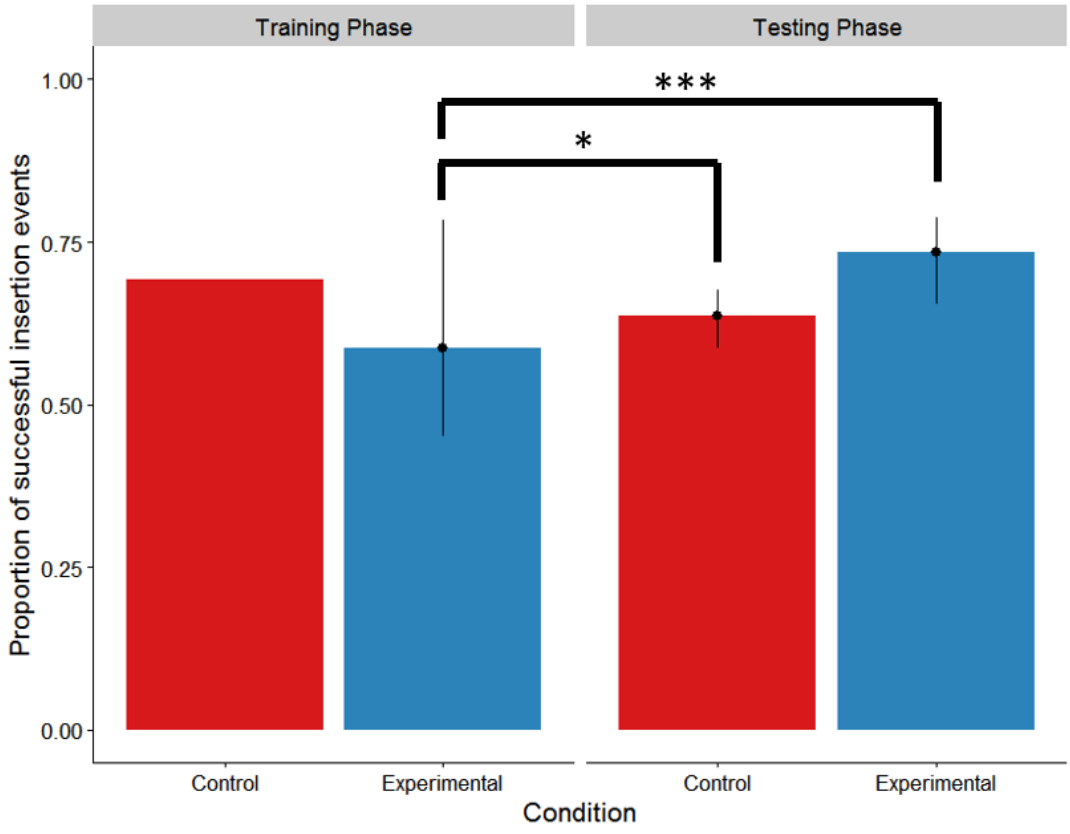


Figure 6.4: Mean proportion of insertion events leading to an eating event in juveniles, per condition per part. Error bars are 95% C.I. (not assuming normality because of proportion). * $p<0.05$, *** $p<0.001$

### 6.4.3 Eating behaviour

#### 6.4.3.1 Training phase (1)

During the training phase, on average, juveniles in the control condition ate less (M = 3.0, SE = 3.0) than juveniles in the experimental condition (M = 18.5, SE = 5.69). There was suggestive evidence of a difference (t(4.39) = 2.41, p = 0.057; see Fig. 6.5, A) and it did represent a large-sized effect (r = .754, 95% C.I. = -0.08, 0.92).

#### 6.4.3.2 Testing phase (2)

During the testing phase, on average, juveniles in the control condition ate less (M=21.0, SE=5.03) than juveniles in the experimental condition (M = 41.74, SE = 5.51). There was suggestive evidence of a difference (t(4.94) = 2.77, p = 0.056; see Fig. 6.5, B) and it did represent a large-sized effect (r = .781, 95% C.I. = 0.06, 0.92).

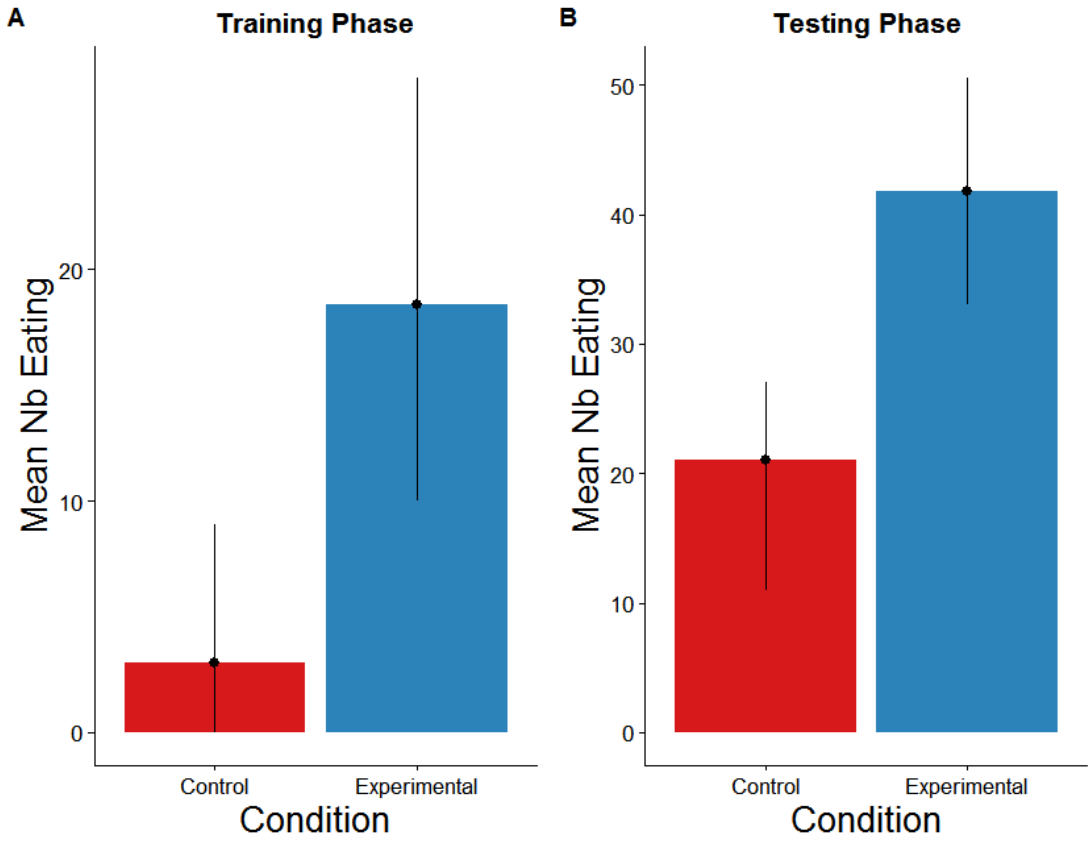


Figure 6.5: Mean number of eating events in juveniles, per condition. Error bars are the 95% C.I. (not assuming normality)

6.4.3.3 Difference

The mean difference in the experimental condition (M = 23.25, SE = 10.19) was higher than that of the control condition (M = 18, SE = 4.04). This difference was not significant (t(3.87) =0.48, p =0.626), however a small to medium-sized effect is not ruled out (r= .236, 95% C.I. = -0.62, 0.78).

Table 6.8: Raw data about juveniles' eating behaviour

| Juveniles | Sex | Condition | Eating Training Phase | Eating Testing Phase | Total Eating | Difference between Training and Testing Phase |
|---|---|---|---|---|---|---|
| AFT3 | F | Ctl | 9 | 27 | 36 | 18 |
| AF3T12 | M | Exp | 34 | 36 | 70 | 2 |
| AF3T4 | F | Exp | 20 | 30 | 50 | 10 |
| AloneT2 | M | Exp | 11 | 55 | 66 | 44 |
| BO2T2 | M | Ctl | 0 | 11 | 11 | 11 |
| BO2T3 | F | Ctl | 0 | 25 | 25 | 25 |
| SuperT1 | F | Exp | 9 | 46 | 55 | 37 |

### 6.4.4 Interaction behaviour (general effect)

6.4.4.1 Training phase (1)

During the training phase, on average, juveniles in the control condition interacted with the novel box less (M=19.00, SE=12.34) than juveniles in the experimental condition (M=74.25, SE=14.39). There was suggestive evidence of a difference (t(4.99)=2.91, p=0.085; see Fig. 6.6, A); and it did represent a large-sized effect (r=.794, 95% C.I. = 0.09, 0.93).

6.4.4.2 Testing phase (2)

During the testing phase, on average, juveniles in the control condition interacted with the novel box more (M = 69.0, SE = 23.81) than juveniles in the experimental condition (M = 66.75, SE = 16.63). This difference was not significant (t(3.82) = -0.08, p = 0.943; see Fig. 6.6, B); and only represented a small-sized effect (r = .040, 95% C.I. = -0.72, 0.69).

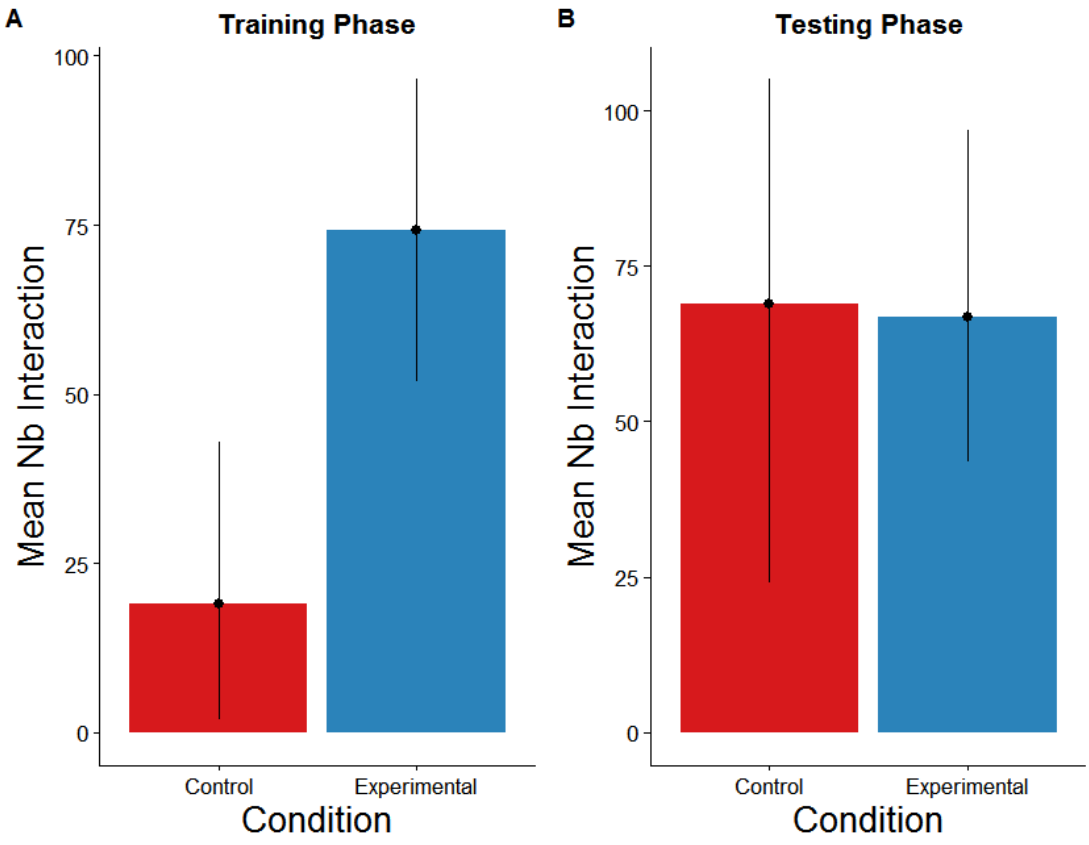


Figure 6.6: Mean number of interaction events in juveniles, per condition. Error bars are the 95% C.I., not assuming normality

6.4.4.3 Difference

On average, juveniles in the control condition increased their interaction with the novel box more (M = 50.00, SE = 21.83) than juveniles in the experimental condition (M = -7.5, SE = 30.73). This difference was not significant (t(4.91) = -1.53, p = 0.202) but it was nonetheless estimated to be a large-sized effect (r = .567, 95% C.I. = -0.85, 0.30).

Table 6.9 summarises the p values for the comparison between experimental and control conditions of all behaviour accordingly (interaction, insertion, and eating), and the corresponding effect sizes.

Table 6.9: p-values of randomisation tests comparing experimental and control conditions for all behaviour and the corresponding effect sizes

| Behaviour | Training Phase | Testing Phase |
|---|---|---|
| Insertion | p = 0.087 (r = .776) | p = 0.143 (r = .628) |
| Eating | p = 0.057 (r = .754) | p = 0.056 (r = .781) |
| Interaction | p = 0.085 (r = .794) | p = 0.943 (r = .040) |

### 6.4.5 Trial by trial analysis: Changes over time

The changes of juveniles' behaviour were examined on a trial-by-trial basis to see whether the differences observed between the conditions were reflected by difference across trials. At the start of the experiment, juveniles in the experimental condition had a higher mean number of interactions (Fig. 6.7, A), insertions (Fig. 6.7, B), and eating behaviour (Fig. 6.7, C), compared to juveniles in the control condition. By the end of the training phase, juveniles in the control condition started to reach the levels of interaction, insertion and eating behaviour observed in the experimental condition (Fig. 6.7 A, B & C). During the testing phase, juveniles in the control and experimental conditions interacted with the box approximately similarly, and continued to do so for the rest of the testing phase (Fig. 6.7, C). Regarding the insertion and eating behaviour of the juveniles in the testing phase, Figure 6.7 B and C show that juveniles in the control condition started lower than juveniles in the experimental condition, but rapidly increased those behaviours to reach the levels of the juveniles in the experimental condition by the last trial, while juveniles in the experimental condition only slowly increased the number of those two behaviours. Because of the patterns seen in Figure 6.7, I ran an *ad hoc* analysis comparing the effect of condition in the first three trials of the testing phase (phase 2) to the effect of condition in the last two (or three, when six trials were conducted in total) trials of the testing phase. "Phase 2.1" represents the first three trials of the testing phase, while "Phase 2.2" corresponds to the last two (or three) trials of the testing phase.

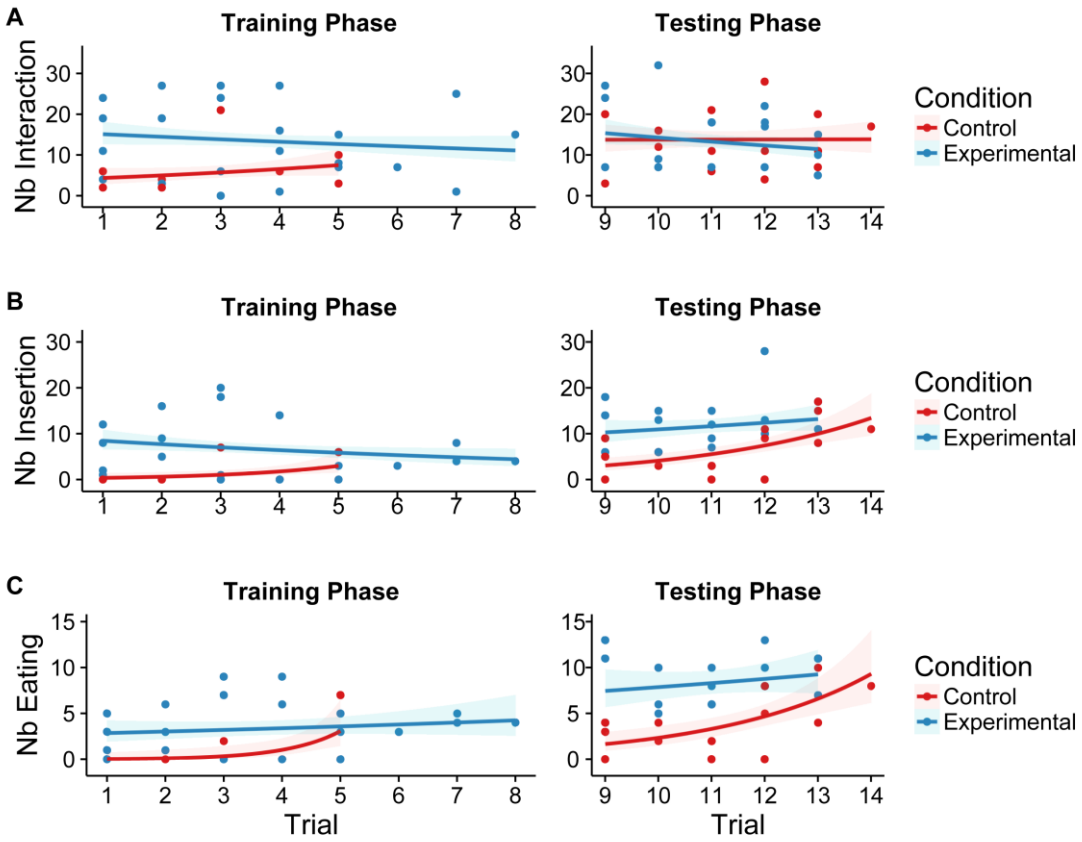


Figure 6.7: Interaction (A), insertion (B) and eating (C) behaviour for each trial, for both conditions (experimental in blue, and control in red). The lines are fitted linear models (method=glm), and shaded areas are the 95% confidence interval (not assuming normality)

I first looked at interaction behaviour. For phase 2.1 it was found that on average, juveniles in the experimental condition (M = 13.83, SE = 4.08) interacted more with the box than juveniles in the control condition (M = 12.23, SE = 4.78). This difference was not significant (t(4.42) = 0.26, p = 0.829); and it did represent a small-sized effect (r = .121, 95% C.I. = -0.82, 0.89).

For phase 2.2 it was found that on average, juveniles in the experimental condition (M = 12.63, SE = 2.43) interacted less with the box than juveniles in the control condition (M = 14.39, SE = 4.95). This difference was not significant (t(2.96) = -0.32, p = 0.714); and it did represent a small-sized effect (r = .284, 95% C.I. = -0.79, 0.90).

I then looked at insertion behaviour. For phase 2.1 it was found that on average, juveniles in the experimental condition (M = 10.50, SE = 1.81) inserted their hand in the box more than juveniles in the control condition (M = 3.22, SE =

1.75). There is suggestive evidence of a difference (t(4.86) = -2.90, p = 0.057); and it did represent a large-sized effect (r = .795, 95% C.I. = -0.21, 0.98).

For phase 2.2 it was also found that on average, juveniles in the experimental condition (M = 13.50, SE = 3.06) inserted their hand in the box more than juveniles in the control condition (M = 10.28, SE = 1.38). This difference was not significant (t(4.09) = 0.96, p = 0.486); and it did represent a medium-sized effect (r = .429, 95% C.I. = -0.70, 0.94).

I finally looked at eating behaviour. For phase 2.1 it was found that on average, juveniles in the experimental condition (M = 7.67, SE = 1.12) ate more than juveniles in the control condition (M = 1.89, SE = 0.99). There is suggestive evidence of a difference (t(4.97) = 3.87, p = 0.056); and it did represent a large-sized effect (r = .866, 95% C.I. = 0.03, 0.99).

For phase 2.2 it was also found that on average, juveniles in the experimental condition (M = 9.58, SE = 1.13) ate more than juveniles in the control condition (M = 6.72, SE = 1.14). This difference was not significant (t(4.77) = 1.66, p = 0.172); however it was estimated to be a large-sized effect (r = .604, 95% C.I. = -0.54, 0.96).

Table 6.10 summarises the p-values for the comparisons between experimental and control conditions of all behaviour according to the set of the testing phase (phase 2.1: trials one to three of the testing phase; phase 2.2: trials four to five/six of the testing phase), and their effect sizes.

Table 6.10: p-values of t-tests comparing experimental and control conditions for all behaviour, and their effect sizes

| Behaviour | Phase 2.1 | Phase 2.2 |
|---|---|---|
| Interaction | p = 0.829 (r = .121) | p = 0.714 (r = .284) |
| Insertion | p = 0.057 (r = .795) | p = 0.486 (r = .429) |
| Eating | p = 0.056 (r = .866) | p = 0.172 (r = .604) |

## 6.5 Discussion

The aim of this study was to examine whether juvenile GLTs could learn about the food-procuring properties of substrates from food-offering calls of adults, thereby testing one aspect of the hypothesis that GLTs are able to teach juveniles. Playbacks of food-offering calls were used to mimic a potential teaching scenario in experiments with wild golden lion tamarins, allowing me to examine whether the learning rate of juveniles was increased by such calls. This was assessed through their foraging behaviour at the novel substrate, particularly through their eating behaviour. In the presence of a novel foraging substrate the foraging behaviour of juveniles that had experienced that substrate with an enhanced rate of food-offering calls was compared to the foraging behaviour of juveniles that had experienced the substrate with normal rates of food-offering calls.

### 6.5.1 Findings

#### 6.5.1.1 Insertion behaviour

It was found that the playback of food-offering calls had an effect on the insertion behaviour of the juveniles during the training phase. Juveniles in the experimental condition that received playback calls inserted their hands into the experimental box more than juveniles in the control condition. The absence of a significant effect in the testing phase could be due to the small sample size (seven individuals). The fact that more insertion events were found in the training phase for juveniles in the experimental condition compared to the juveniles in the control condition, means that food-offering calls have a direct effect on juveniles' tendency to interact with the most relevant part of the box.

In most cases individuals increased their rate of insertion behaviour from the training to the testing phase (Table 6.2), which could reflect habituation to the box or associative learning about its food.

#### 6.5.1.2 Probability of success of an insertion event

In principal, calls could also influence the probability of success of insertion events, for instance, by enhancing processing skills, or, more realistically, by increasing perseverance and motivation to obtain food from the substrate. I used the proportion of an insertion event leading to an eating event as a measure of perseverance. However, no effects of playbacks of food-offering calls were found on the probability of success of an insertion event. Food-offering calls could attract juveniles to a foraging location, but subsequently the pattern of foraging exhibited at that location was seemingly not influenced by the calls. Moreover, once individuals have inserted their hand in the box, it becomes quite easy for them to obtain food, imposing a ceiling on success and therefore explaining our results.

An effect of the phase was found on the probability of success of insertion events. In the testing phase juveniles were more successful at obtaining food once they had inserted their hands, than in the training phase. This suggests that either 1) juveniles have learned how to manipulate the box more efficiently through personal experience with that box, or that 2) being older in the testing phase they have gained manipulative and extractive skills outside of the experiment, which they are now using in this specific context.

#### 6.5.1.3 Eating behaviour

When directly examining the eating behaviour in the two conditions, there was a significant effect of the food-offering calls. Juveniles in groups that received the food-offering calls ate more food from the box than juveniles that did not have a playback. This was found in both the training and testing phases. There was also a weak significant difference between the two conditions. It seems likely that there are some direct effects of the training phase on the testing phase, as it is unlikely that long-term effect of playback calls would be obtained without any short-term effects first.

If juveniles in the experimental condition have learned from the food-offering calls, it would be expected that they eat more than juveniles in the control condition, especially in the testing phase. The results found support this hypothesis. It would also be expected that the increase in number of food items eaten in the testing phase would be greater than in the control condition. This was however not supported by our results (no significant difference between the difference in the testing and training phase for the juveniles in the experimental and control conditions), suggesting that juveniles from the control condition catch up with the number of eating events of juveniles from experimental condition and that playbacks allow learning to be accelerated.

#### 6.5.1.4 Interaction behaviour

Looking at the specificity of the playback effect, I wanted to know whether the effects of food-offering calls would be quite general, by attracting attention to the box and encouraging interaction with it, or quite specific, by encouraging interaction with a specific part of the box (insertion) and obtainment of food (eating). When directly analysing the effect of playbacks on interaction with the box, I found the food-offering calls encouraging juveniles to interact with the box to obtain food. This was found only during the training phase, and this effect did not persist into the testing phase. Therefore there seemed to be a direct and immediate effect of the calls on the rate at which juveniles interact with the box, whilst those calls are being played (training phase). This might allow them to become more familiar with the box, and learn its food affordance through stimulus enhancement. As the results suggest, if the calls directly influence the juveniles' interaction with the box when they are played, this could then lead to more insertion and eating events.

#### 6.5.1.5 Summary of findings: direct vs long-term effects of food-offering calls

In sum, during the training phase (immediate effect of food-offering calls, as a potential attractor to the box), I found suggestive evidence that juveniles in the experimental condition that experienced playbacks interacted more, inserted their hand into the box more, and recovered more food items from the box than

the juveniles from the control condition (no playback). Therefore, playback calls seemingly have a direct and immediate impact on the approach behaviour of juveniles, as well as on their foraging behaviour. The effect of food-offering calls on approach behaviour in juveniles has been observed in previous studies, but has previously never tested through playbacks (Boinski et al., 1994). Moreover, the effect of food-offering calls on foraging success has also been described in the wild, but never directly tested (Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002). Consequently, there is suggestive evidence for an immediate effect of food-offering calls on juveniles' foraging efficiency.

In addition, I then examined the long term consequences of those food-offering calls: whether, once independent, juveniles were more likely to forage (successfully) from the novel substrate if they had had more experience of this novel substrate with a higher rate of food-offering calls when younger, than if they had not. There was little evidence for an effect of food-offering calls on interaction and insertion behaviour, but in the testing phase, juveniles that had experienced playbacks when younger (experimental condition) ate more from the box then did the juveniles that had not experienced the playbacks.

Therefore, food-offering calls seem to directly impact juvenile's interaction with the box, and potentially reduce their neophobia. Increasing the attraction towards the box in the training phase could lead to an overall increase in insertion behaviour and focus on the right part of the box to obtain food, which are the results obtained, leading to an increased eating in the experimental condition when the juveniles are independent (testing phase; but also overall). This would suggest that playback of food-offering calls seems to have long lasting effects on the juveniles' efficiency to obtain food from the substrate. These findings are consistent with teaching about the substrate on which to forage on, through stimulus enhancement, but further investigation of the first two criteria of Caro and Hauser's (1992) is necessary for food-offering calls to be considered teaching in this context.

#### 6.5.1.6 Trial per trial analysis

From the graphs showing the interaction, insertion and eating behaviour across trials, juveniles in the experimental condition interact, insert and eat more from the box than juveniles in the control condition from the very first trial in the training phase. This further supports the immediate effect of food-offering calls. It can also be seen that the number of interaction events is more or less constant for both conditions in the testing phase. However, when looking at insertion and eating events, the numbers of events increase, especially in the control groups, in the testing phase. In the testing phase, there seems to be a difference between conditions in the first three trials, with juveniles in the experimental condition inserting and eating more than juveniles in the control condition. However, at the end of the testing phase, the control groups caught up with the experimental groups in the number of insertion and eating events.

When running the post-hoc analysis comparing the conditions in the first three trials of the testing phase, versus in the last two/three trials, it was found that the control and experimental groups only differed in the first few trials in their eating and insertion behaviour, but not in their interaction behaviour. Moreover, the eating, insertion and interaction behaviour of juveniles in the two conditions in the last trials of the experiment were not significantly different from each other. This could be explained by the fact that interaction behaviour is not reinforced by a positive reward, and therefore remains constant without the presence of food-offering calls, while the insertion and eating behaviours are being reinforced by successful foraging. At the beginning of the testing phase, the numbers of successful foraging events were higher in the experimental condition, potentially because of the effects of the playbacks during the training phase. However, by the end of the testing phase, the numbers of insertion and eating events of the control group had increased to reach the levels of the experimental groups. This might be due to the positive reinforcement of foraging success. I suspect that reinforcement from the foraging success was also happening in the training phase but that it was accelerated in the experimental group because of the food-offering calls, playing a role through stimulus

enhancement. This suggests that juveniles direct their attention towards the important parts of the box because those behaviours are reinforced by food consumption, and that learning is accelerated by the playbacks that direct the juveniles' attention towards the box.

### 6.5.2 General points

#### 6.5.2.1 Limitations

One limitation of the experiment was the low sample size. This arose because only groups of GLTs that were habituated to regular human contact could be used for the experiment, and only six such groups were easily accessible. Initially, there were 10 juveniles across those 6 groups, but in one of those six groups (AF2) a pair of twins disappeared just before the start of this experiment (February 2014), and in another group (Alone) one of the twins disappeared between the training and testing phase of the data collection. This means that the analysis is based on seven juveniles from five groups (BO2 and AF3 had twins), which mean that my findings must be interpreted with caution. Given the small sample size, it is hard to draw definitive conclusions from this data set. In fact, several of my results show no significant effects but very large-sized effects, suggesting that the absence of strong evidence observed is likely to be a result of the sample size and low statistical power. Bigger sample sizes would be necessary to get a clearer interpretation of the results, however it was found that juveniles learn about the appropriate substrate on which to forage from stimulus enhancement.

A further potential limitation of the experiment is the use of playback stimuli calls from individuals that are unknown to the juveniles. It is not known whether GLTs distinguish between familiar and unfamiliar food-offering calls, nor whether the juveniles would behave differently if they did. In captivity, GLTs are capable of identifying the sex of an individual fifteen seconds after playback of their vocalisation (French & Inglett, 1989). There might therefore be some personal information in tamarin calls that allows an individual to identify callers. Moreover, cotton-top tamarins are able to discriminate between a familiar and

unfamiliar individual emitting a long-call (Snowdon, Cleveland, & French, 1983). However, to my knowledge, there are currently no data showing that GLTs can recognise individual callers from food-offering calls. Moreover, adults are quite tolerant to juveniles from other groups: adults let juveniles from other groups play with their own juveniles without interfering, and occasionally even let juveniles from other groups take food from them (pers. obs). Given this tolerance, it is likely that the familiarity of the calls would not influence the juveniles' behaviour, but this is an issue for further experimentation.

Ruiz-Miranda et al. (2002) also point out that in GLTs, although the behavioural responses to long-call playbacks are indistinguishable from responses to naturally occurring long-calls, the vocal response differed slightly, mainly in some acoustic frequency measures. There are no data showing that this might be the case in response to food-offering calls, but since behavioural responses to calls were analysed, I expect that there should be no difference in response to playbacks and naturally occurring calls.

#### 6.5.2.2 Future work

I determined that juveniles' learning of what substrate to forage on is accelerated by food-offering calls. However, to determine the specificity of the effect of the food-offering calls, two more conditions could be added to the experiment. The first one would be a condition where juveniles are exposed to the box in the presence of playbacks of white noise or sounds from the environment. This would allow me to determine whether the effect observed is due to a playback being emitted (if we see similar effects in the white noise playback condition and the food-offering call playback condition), or whether it is due to a playback of food-offering calls (if we see similar behavioural response in the white noise and control condition). The second would be a condition where juveniles are exposed to the box in the presence of playbacks of food calls. Boinski et al. (1994) observed that individuals will approach a group member when it emits a food-offering call (called tsick calls in their paper) but not a food call. This would allow use to directly test this observation, and determine

whether the results obtained in this experiment are due to the effect of food-offering calls (if we find different behavioural response for juveniles in the food-offering call and food call condition) or whether those effects are due to the presence of calls from a conspecific in a foraging context (if we find a similar effect of food-offering calls and food calls).

Very little is known about individual recognition in GLTs from vocal communication (but see French & Inglett, 1989). It would be interesting to know whether juveniles respond differently to caller identity. This could be tested by using playbacks of 1) unknown individuals; 2) familiar individuals but members of a neighbouring group; 3) mothers; 4) fathers; 5) non-related helpers (group members); and 6) related helpers (siblings, group members). As mentioned in 5.5.2.1, I expect no effect of the caller identity on the behavioural response of the juveniles.

Moreover, the box used in this experiment was the same in the training and the testing phase. Hence, it is possible that the juveniles learn something specific about this box, rather than more generalizable knowledge about what kind of substrates are good for foraging. When Rapaport reports the use of food-offering calls in a new context, the substrate was similar for each observed event (concealed within vegetation) but the vegetation varied slightly (crevices in vines, knotholes in branches, dead leaves…) (Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002). Hence, given the environment in which GLTs forage in, I suspect that juveniles generalise to a certain extent the type of substrate in which to find prey, given that they are quite similar. This however remains to be tested. One way to do this would be to have groups trained to forage from a particular box in the presence of food-offering calls, and then test half of the groups on this same box, similar to what I did in this experiment, while testing the other half on a novel box that is similar in colour, shape or texture to the box on which they were trained, but slightly different. If differences in foraging behaviour are found between the two conditions, it would indicate that GLTs acquire specific knowledge about a particular substrate, but if no differences are found, it would indicate that GLTs generalise their knowledge to similar substrates.

#### 6.5.2.3 Comparison with pied babblers

Pied babblers teach their young to associate the purr call with food delivery (Raihani & Ridley, 2008). Nestlings learn to respond to purr calls: in a playback experiment, when more calls are played paired with food delivery, nestlings respond sooner than when calls are not paired (Raihani & Ridley, 2008). The results from Raihani and Ridley (2008) suggest that adult pied babblers teach their young to associate purr calls with food delivery, potentially to precipitate fledging. However, as seemingly seen in GLTs (Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002), Radford and Ridley (2006) found that adult pied babblers also modify the context in which they use the purr calls according to the developmental stage of the young. First the adults use offering calls to facilitate transfer of food to the young (Raihani & Ridley, 2008), and when the young are mobile, adults use the calls to recruit them to a profitable foraging site (Radford & Ridley, 2006). When fledglings responded to the purr call by going to the new foraging location, they spent more time at this location and experienced a greater foraging success (Radford & Ridley, 2006). It is possible that in the second context, adults use the purr calls for a separate function: to recruit fledglings to a good foraging patch. In this context, no learning needs to occur. It is possible that the same could be true for GLTs: adults could teach their young to associate food-offering calls with food delivery (since those calls are mainly used prior to food transfers), and that the learning observed in this experiment is a by-product of adults attracting juveniles to a good foraging location so that they can obtain some nutriments, instead of adults teaching juveniles to forage on specific substrates, as proposed by Rapaport (2011). In fact, unlike pied babblers who regularly use their purr calls to attract juveniles to a location (0.6 times/h) (Radford & Ridley, 2006), GLTs only rarely use food-offering calls to attract their juveniles to a particular substrate. It would therefore be interesting to investigate how juveniles learn to associate food-offering calls with the presence of food, and whether the adults actively modify their behaviour to facilitate their learning, as seen in pied babblers.

#### 6.5.2.4 Food calls in tamarins

In conclusion, there is evidence that the food-offering calls of GLTs facilitate learning of which substrates to forage from. The findings of this experiment are consistent with the teaching hypothesis, as hypothesised by Rapaport (2011). She initially proposed that as the juveniles grow older, adults start using food-offering calls to direct the juveniles' attention towards a particularly profitable substrate. Lion tamarins have a high reproductive turnover strategy: they show intense parental investment towards offspring, have multiple births per year of twins, and mature rapidly (K. Brown & Mack, 1978). In anthropoid lineages, the high success of survival and reproduction is in part due to learning occurring during a long maturation period. Teaching in GLTs could therefore be a strategy to speed up learning valuable skills and information, and thereby reduce the burden of provisioning by hastening the transition to independent foraging. Roush and Snowdon (2001, p. 415) hypothesised that in another species, cotton-top tamarins, food calls could create "*an opportunity for infants to learn not only what foods are appropriate but what vocalisation are appropriate in feeding contexts*", and suggested that adult tamarins transmit information to group members about the quality and location of food.

Although food elicited calls have not been extensively studied in GLTs, more than three decades ago Brown and Mack (1978) showed that adults who possessed food items emitted calls that stimulated other individuals to approach. Moreover, Boinski et al. (1994) found that there were no differences in the use of calls comparing age (subadult versus adult), sex, or age of nearest neighbour, and few group differences in call use in wild GLTs. Hence, call types are used similarly by most individuals in this species. This suggests that GLTs may use vocalisations as honest signals of their location and activity, since each vocalisation was also associated with a specific ecological context. The honesty of the vocalisation could help group members coordinate their movement and activity, and facilitate cooperation (Boinski et al., 1994). Such findings support our conclusion that food-offering calls are an honest signal used to attract

juveniles to a specific substrate on which it is profitable to forage, and about which they learn through stimulus enhancement. However, the question still remains as to whether the learning observed in my experiment is the function of the calls (i.e. teaching) or whether it is a by-product of (allo-)parental care. In fact, an alternative explanation for the modified context in which GLTs use the food-offering calls is that the calls are used to attract juveniles to a location where juveniles can forage, saving the adults time and energy compared to a food transfer. This chapter only examines the third criterion of Caro and Hauser (1992) teaching definition. Further analysis of the first (because only 15 instances of this behaviour have been reported in the wild) and second criteria are necessary to establish the function of the calls in this modified context.

# Chapter 7:

# A follow up on Nicol and Pope's (1996) study: evidence for teaching behaviour in domestic fowl?

## 7.1 Abstract

This chapter examines whether the maternal foraging display in domestic chickens can play a role in teaching young chicks which food to forage on and which food to avoid. In this study, a similar experimental design to Nicol and Pope's (1996) was used to replicate and further analyse their findings that hens increase their food pecking, ground pecking and ground scratching behaviour when observing chicks seemingly making foraging errors. The experimental design from Nicol and Pope (1996) was modified slightly to allow investigation of the chicks' behaviour, particularly looking at their foraging decisions and how they might be affected by the hens' behaviour. Although I found that hens did not modify their foraging display based on the chicks' foraging errors, the 95% C.I. showed little evidence that the pattern of results obtained were inconsistent with Nicol and Pope's (1996) findings. I found a weak correlation between the chicks and hens' foraging choices which was not in the expected direction: hens seemed to adjust their dietary choices based on the chicks' choices. Finally, I found that chicks were consistent in their foraging decisions up to 10 days after the demonstration.

## 7.2 Introduction

### 7.2.1 Social learning and social influence in domestic fowl chicks

As seen in Chapter 3, domestic fowl can acquire a lot of information from other individuals, and this ability may start in the first day of life. Young chickens are precocial, and hatch with highly developed brains. However, during the first few days of their life, chicks are insensitive to the reward of ingestion, so they are likely to peck at both edible and inedible particles (Hogan, 1984). Thus, social influence seems necessary to direct the chicks' attention to particular particles that are edible. Studies have shown that in juvenile birds, food choices can be affected by both social stimuli and social learning (Midford et al., 2000; Moffatt & Hogan, 1992; Sherry, 1977; Stokes, 1971).

#### 7.2.1.1 Social influence of the mother hen

Social influences have an important role in the development of this species. The mere presence of a hen increases the pecking behaviour of chicks (Wauters et al., 2002), potentially by lowering the need for vigilance. The presence of a hen when growing up also leads pullets to be less neophobic around novel objects (Perré et al., 2002). Moreover, Wauters et al. (2002) found that the feeding activities of hens and chicks were correlated: when a hen had a high level of active feeding, so did her chicks.

Both in red junglefowl and domestic fowl, the mother hens' behaviour can also affect the foraging choices of their chicks. Hens have a multimodal display that combines pecking movement and food calling, called "tidbitting", which attracts the chicks to their location (Clarke, 2010; Marler et al., 1986b; Sherry, 1977). This allows the hens to influence the feeding behaviour of chicks by attracting them towards suitable food (Allen & Clarke, 2005; Moffatt & Hogan, 1992; Nicol, 2004, 2006). Some studies have shown that chicks are sensitive to the vocalisations in the display and their quality (Guyomarc'h, 1974; Moffatt & Hogan, 1992). When there is a food call present in the display, the chicks' response is more pronounced then when there is no food call (Wauters & Richard-Yris, 2002). Hens have strong food preferences and when they have chicks they express those preferences through food calls (Wauters & Richard-Yris, 2002; Wauters et al., 1999, 2002). When the hen finds high quality food, she emits longer and more intense food calls, which attracts chicks to the area more rapidly compared to calls elicited for low-quality food (Moffatt & Hogan, 1992). This can have a short-term influence on the chicks' diet selection and quality; but it is not known whether chicks retain information about food palatability or quality from the hens' vocalisation in the long-term or when the hen (stimulus) is no longer present.

Wauters and Richard-Yris (2002) also found that the chicks' response to food calls increased and was faster as they grew older. This, in combination with Guyomarc'h's (1974) findings that the behavioural response of chicks varied

with their experience rather than their age, suggests that chicks learn the conditions associated with food calls.

Regarding the pecking movement, many studies claim that the chicks peck where the hen pecks (Collias, 1952; McBride et al., 1969; Stokes, 1971; Wood-Gush, 1971). In an experiment, Wauters and Richard-Yris (2002) showed that after approaching a hen as a response to the food call and pecking display, chicks increased their pecking and directed their pecking preferentially towards the dish the hen was feeding on. They also did so simultaneously with the hen, suggesting that the display directs the chicks' attention to the food chosen by the hen through local enhancement (Wauters & Richard-Yris, 2002).

Hence there is a strong influence of the hens' foraging behaviour on that of her chick, but in most experiments the chicks' reactions are immediate, so it is not known whether the chicks would be attracted to similar food to that chosen by the hen (stimulus enhancement) or if the preferences expressed by the chicks extend after the mother-young link has been broken or when the hen is no longer present, which would be indicative of learning.

In a closely related species, the white-tailed ptarmigan, Allen and Clarke (2005) found stronger evidence of long-term transmission of information between hens and their chicks, through the help of food calls. In fact, similar to domestic chickens and Burmese red junglefowl, the white-tailed ptarmigan food call elicits chicks to join the hen and consume specific food (Clarke, 2010; Marler et al., 1986b; Sherry, 1977). Hens called for their chicks after choosing particular food patches, usually containing plants with high levels of protein. Chicks preferentially fed on plants for which the hens had emitted food calls: the chicks' diet was positively correlated with the hens' food calling, not plant abundance (Allen & Clarke, 2005). Those preferences seemingly lasted in the population for at least two years, indicating social learning, which coincided with Caro and Hauser's (1992) third criteria of the teaching definition (Clarke, 2010). Moreover, white-tailed ptarmigan tidbitted only in the presence of naïve chicks and displayed more in the presence of high-protein plants. However, hens

themselves did not feed more on high-protein plants compared to other plants and did not consume the items they tidbitted, thus coinciding with the first and second criteria of Caro and Hauser's (1992) definition. This is similar to the behaviour of domestic hens who alter their foraging display when perceiving chicks consuming seemingly unpalatable food (Nicol & Pope, 1996). Consequently, experimental work in white-tailed ptarmigans is consistent with this species engaging in teaching, but the author notes that more work still has to be carried out, particularly on the first two criteria, to consider the ptarmigan's maternal display as teaching behaviour (Clarke, 2010). In fact, although mothers where observed to only tidbit in the presence of chicks, and were observed not to ingest the food, the author claims that a more compelling demonstration of hens modifying their display based on chicks' difficulty to consume high-protein food, as observed in meerkats (Thornton & McAuliffe, 2006) and domestic fowl (Nicol & Pope, 1996), would be necessary to consider the white-tailed ptarmigans' behaviour as teaching. Moreover, following Hoppitt et al.'s (2008) suggestion, Clarke (2010) claims that evidence that the tidbitting display has been modified to promote learning in the young, rather than promote the young's acquisition of nutritional supplies, is necessary for the behaviour to be considered teaching.

#### 7.2.1.2 Social influence and learning from artificial hens and arrow models

Further work with artificial hens as models has focused on the effect of the model's pecking behaviour on the observer showing that an angular stimulus making pecking movement was sufficient to direct pecking in naïve chicks (Suboski & Bartashunas, 1984; Turner, 1964). For instance, as the pecking rate of a model increased, so did the pecking rate of chicks (Tolman, 1967b). This was especially the case when there was an auditory stimulus (tapping sound) as well as a visual stimulus (pecking movement). The tapping sound alone did not seem to have any effect on the chicks. These findings are consistent with the more naturalistic studies with real hens as models. Similar findings were reported by Suboski (1984), where chicks increase their pecking behaviour after observing a mechanical arrow "pecking" at a stimulus. Turner (1964) further showed that

neonatal chicks are attracted to the site of a pecking model, and peck near it. If there are two choices of stimuli available, neonatal and day-old chicks preferentially peck at similar objects to the one that the model is pecking at, as an immediate response (Suboski, 1984; Suboski & Bartashunas, 1984; Turner, 1964). This response by the chicks persisted after the model or stimulus was removed, suggesting stimulus enhancement (although the model and stimulus were removed only 8 to 9 minutes after they had been operational). Further work from Bartashunas and Suboski (1984) has shown that the preference gained by chicks from observing a rod "pecking" at a particular stimulus can last at least three days. This suggests that learning through observational conditioning and stimulus enhancement might play a role in the acquisition of foraging preferences in chicks when the demonstrator is an artificial rod. Further results suggest that the arrow directs the pecking of the chicks (Suboski & Bartashunas, 1984). Although Suboski and Bartashumas (1984) have shown that an artificial "pecking" rod can influence the chicks pecking preferences, this is not the case for adult hens (Nicol & Pope, 1992). This supports the notion that, with growing experience of conspecifics, either the use of social learning changes, or the perception of an artificial model as a real conspecific is altered. In fact, with experience of conspecifics, chicks pay less attention to mechanical rods or hens, compared to chicks with no experience with conspecifics (Turner, 1964). This suggests that the behaviour of a maternal hen could potentially have different effects on the chicks' foraging behaviour than a mechanical model.

#### 7.2.1.3 Social influence and learning between chicks

The role of the mother hen is important in guiding their chicks to eat the correct food, but as the chicks grow older, they start relying more on their flock mates for social information (Nicol, 2015). For instance, similar to the effect of the presence of a hen, the mere presence of another chick increases the amount of food a chick ingests, especially if the other chick is actively feeding (McQuoid & Galef, 1993; Tolman, 1968; Tolman & Wilson, 1965). Tolman (1968) suggest that the presence of a conspecific could reduce fear. It could also lower the need for vigilance behaviour.

Compared to the previous experiments which included one naïve chick and one demonstrator chick, similar findings were reported in groups of chicks where either a knowledgeable or a naïve demonstrator was present. Both when chicks were foraging with a knowledgeable demonstrator, and on subsequent trials where they no longer had a demonstrator, subjects consumed more food than chicks that had been paired with a naïve demonstrator (Gajdon et al., 2001). Chicks with trained demonstrators also showed a clear preference for the demonstrated food, even after the demonstrator was removed (Gajdon et al., 2001). Similar findings were reported with older chicks: when observing an individual (or a video of an individual) feeding from a particular dish or location, chicks of a few weeks of age will approach similar dishes and locations (McQuoid & Galef, 1992, 1993). This is evidence of social learning between chicks of fairly similar ages.

Day-old chicks have also been found to learn to avoid unpalatable food by watching another chick's disgust reaction (Johnston et al., 1998). Their avoidance lasted for at least 24h. This shows that young chicks pay attention to the responses of others towards novel food. Those results were confirmed with 2-day-old chicks of a different strain, suggesting that the ability to avoid pecking at a food item that has elicited a disgust reaction in a conspecific might be robust across the species (Salva et al., 2009).

Other experiments have shown that chicks are also able to learn aggregative behaviour as a result of social interaction (Baron & Kish, 1960). Moreover in a feeding context, the presence of a chick at a feeding trough for at least 15 seconds will double the chance of another individual joining it, compared to joining a trough where no individual is present (Collins & Sumpter, 2007).

#### 7.2.1.4 Concluding remarks on social learning in young chicks

In gallinaceous birds, signals surrounding foraging behaviour are likely to be important in the development of the young (Allen & Clarke, 2005; Collias,

1987; Evans & Marler, 1994; Marler et al., 1986a, 1986b; Moffatt & Hogan, 1992; Sherry, 1977; Stokes, 1971; Wauters et al., 2002). Chicks have an unlearned predisposition to peck at objects resembling food (Suboski & Bartashunas, 1984), but chicks learn to distinguish edible from inedible food through the help of visual and auditory cues from other individuals (Johnston et al., 1998; McQuoid & Galef, 1993; Nicol & Pope, 1994, 1996; Turner, 1964; Wauters & Richard-Yris, 2002; Wauters et al., 1999). The hen's behaviour might play a particularly important role in shaping chick foraging behaviour, encouraging them to peck at specific food sources. For instance, observational conditioning might be an important mechanism that allows young chicks to acquire foraging preferences (Nicol, 2004). However, there is still a lack of data showing long-term effects of hen's behaviour on their chicks' foraging decisions.

There is strong evidence that in the short-term, the foraging behaviour of young chicks can be influenced by their mother hen (Sherry, 1977; Stokes, 1971), chicks of the same age (Johnston et al., 1998; Moffatt & Hogan, 1992; Tolman, 1964; Tolman & Wilson, 1965) and artificial pecking activity (Bartashunas & Suboski, 1984; Suboski & Bartashunas, 1984; Tolman, 1967b; Turner, 1964). Moreover, there is evidence that preferences are retained after the demonstrator is removed, in some cases up to three days after the removal of the demonstration, indicative of social learning. However, this has only been found when the demonstrators are either chicks of a similar age, or an artificial rod where the "behaviour" expressed is vertical pecking motion. Although highly likely, it still remains to be shown that social learning occurs between the mother hen and her chicks. Hens exhibit a fuller range of behaviour compared to pecking rods, and the demonstration of foraging choice could be less clear when mixed with other behavioural signals the hens might display, or to the contrary enhance it.

Moreover, although, young chicks seem to heavily rely on social influence when it comes to foraging behaviour, this changes as the individuals get older. Adult chickens seem to rely on previous experience about food palatability (Nicol 2004). For instance, although Johnston et al. (1998) found that chicks

learn to avoid unpalatable food through observation, Sherwin et al. (2002) found that 9 week old pullets do not avoid pecking on unpalatable food after watching a conspecific's disgust reaction. However, as mentioned in Chapter 3, adult hens are still able to acquire important information through social learning. Although artificial rods or models have an impact on chicks' foraging decision, those do not seem to have the same impact in adult hens suggesting that a social model is critical (Nicol & Pope, 1992). Young chicks might be particularly attentive to the behaviour of conspecifics while older chicks might rely more on their own experience.

### 7.2.2 Domestic fowl's feeding display is sensitive to perceived chick error (Nicol & Pope, 1996)

Hens increase the intensity of their foraging display when chicks are present (Sherry, 1977), when they move too far away, fail to respond (Stokes, 1971), or when chicks are physically separated from the hen (Wauters et al., 1999). This suggests that hens are sensitive to social context. Nicol and Pope's (1996) experiment looked at whether hens, in addition to adapting their display to the sight and proximity of chicks, would modulate it based on the chick's behaviour. The study investigated whether chicks had acquired the correct information about food palatability from the hens' display (Nicol, 2004).

In their experiment, Nicol and Pope (1996) trained 12 hens to learn that a food colour was palatable while the other was not. These hens were then either faced with (1) chicks that had been trained to feed on a food colour that was palatable to the hen, making no apparent feeding error, or (2) chicks that had been trained to feed on a food colour that was unpalatable to the hen, hence making apparent errors. Both foods were actually palatable when the chicks were feeding. Although there was no sign of an effect of the chick's foraging choice on the hens' vocalisation, there was an effect on other aspects of the maternal foraging display. The hens responded more intensely to chicks that made apparent errors compared to those that did not: they increased their food pecking rate when food was available, and their ground pecking and ground

scratching rate when no food was available. This implies that hens were sensitive to the feeding errors made by their chicks.

As the chicks were eating palatable food at all times, the hens did not react to a disgust reaction of the chicks, but rather to a combination of the hens' own knowledge about the food palatability and her chicks' feeding choice. An increase in display usually makes the chicks increase the speed in which they approach the mother in an attempt to peck at the food she is demonstrating (Moffatt & Hogan, 1992). However, in this experiment chicks and hens were separated, so chicks could not directly access the hen's food.

Nicol and Pope's (1996) experimental results suggest that the foraging display of the hens is made to attract chicks towards palatable food and to direct the chicks' attention away from unpalatable choices (Nicol, 2004). This shows that the maternal display is not fixed but can be flexibly adjusted according the chicks' knowledge of their environment (Nicol, 2006).

### 7.2.3 Aim of this experiment

Nicol and Pope (1996) showed that hens' modified their behaviour based on perceived errors made by the chicks, fulfilling the first criterion of Caro and Hauser's (1992) teaching definition. The aim of my experiment was twofold:

1. **To replicate Nicol and Pope's (1996) findings**.
2. **To assess whether chicks change their behaviour based on the hens' behaviour (third criteria of Caro and Hauser's (1992) definition). Particularly, the aim was to test whether chicks preferentially forage from similar food to that of the hen**. This was done in two steps:
   2.1 **When the hen was present (conditioning).**
   2.2 **On four days after the conditioning when the hen was no longer present, to test how long the social effect would last.**

The chicks' foraging choices were assessed on five separate occasions in order to determine whether the hens' behaviour had immediate effects on their

chicks' behaviour as well as long-term effects (up to 10 days after the demonstration).

When chicks eat seemingly unpalatable food, an increase in active behaviour (food pecking, ground pecking and ground scratching) is expected in the hen (Nicol & Pope, 1996). It is also expected that chicks acquire the same food preference of their mothers, even if this requires them to switch preferences. If their initial preference is opposite to that of the hen, I expect the switch to the hens' preference to take more time, but I expect the chicks to switch their preference nonetheless. If teaching of acquired preferences occurs, and chicks learn from the hens, then this is expected to remain for at least several days.

## 7.3 Methodology

### 7.3.1 Subjects

12 broody hens (Silkie, n= 5, Indian game crossed with Australorp, n= 5, Silkie crossed with Pekin Bantam, n= 2), were obtained from a breeder and housed individually in a floor pen (1.5 × 1 m) at the Langford Campus of Bristol University. The pen was bedded with wood shavings and contained a feeder with plain brown chick crumbs, a drinker and a cardboard nestbox. Temperature in the floor pen was maintained at 23 °C and the lighting schedule was 12L:12D. Each hen was given six fertile eggs obtained from a commercial broiler breeder farm, meaning the hens and chicks were unrelated. Between four to six of those eggs hatched, and two pairs of chicks were used in the experiments for each hen. 12 hens were used as this is the number of hens that Nicol and Pope (1996) use , and I was unable to increase this number due to time constraints.

### 7.3.2 Procedure

#### 7.3.2.1 Habituation and training

As soon as they hatched, chicks were habituated to human presence (day 1) and handling (day 2). Handling consisted of picking up chicks while they remained in visual and auditory contact with the other chicks and the hen. On

the second day, the chicks were also habituated to short time (10 min) separation, and separations through mesh wires (10 min), where the chicks and hen were in auditory and visual contact, but not physical contact.

On their third day, training for both chicks and hens began. On each training day, food was removed in the morning from the home pen 2:30 hours prior to the first training session. Both hens and chicks were trained three times a day (late morning, early afternoon, late afternoon). Their usual feed was placed back in the evening, once their last training session was finished. Training occurred for a minimum of three days (to allow the chicks to be old enough and used to feeding in the absence of the hen) and until the hens pecked on the palatable food for 90% of the time on the last training session. Post-experiment, video analysis was then carried out on this session to establish whether or not the hens were sufficiently trained (see below).

Each hen was randomly assigned to a treatment: trained on red food, yellow food, or both. They were trained in a separate pen (no visual contact with the chicks during training, and reduced auditory contact), and presented with two circular dishes (20 cm diameter). One of each dish contained red-coloured feed, while the other contained yellow-coloured feed. The feed was coloured with food colouring. The dishes had coloured cardboard taped on the sides so that they were the same colour as the food they contained. One dish of coloured feed had been made unpalatable by adding 16 mg/100 ml of quinine hydrochloride. First I tried the same concentration as used in Nicol and Pope (1996), but that did not change the behaviour of the hens, so I doubled the concentration. Hens trained on red were given palatable red feed with the yellow feed made unpalatable, while hens trained on yellow had the red food made unpalatable. Untrained hens were given palatable food of both colours.

Four hens were trained on red feed, four on yellow feed and four (untrained) hens were given both foods. This meant that I tested a total of 12 hens, the same number as in Nicol and Pope (1996). The hens' feeding behaviour during the training phase was recorded and analysed, to make sure the hens

passed the qualifying criteria. Hens passed the criteria if they pecked at the correct (palatable) coloured food more than 90% of the time, during the last training session, both in terms of total time spent pecking and total number of pecks.

For each hen, two pairs of chicks were randomly allocated to two training regimes: red or yellow. The same pairing was used for each of the training, conditioning, and testing sessions. The colours used for training were counterbalanced, and randomly assigned. Training for each pair occurred in a different pen, with no visual contact with each other or the hen, and reduced auditory contact with the hen. The chicks' training was different to the hens' as the chicks were to have no prior knowledge that one feed was aversive. Hence their training consisted of habituation to one colour. Chicks' training was performed in pairs. For each hen, while two chicks were presented with yellow coloured chick crumbs in a yellow bowl, the other chick pair was presented with red coloured chick crumbs in a red bowl. During training, the pairs could not see each other.

Each hen's brood of chicks was split into three groups, which were: (1) chicks trained on "similar" food colouring to that of the hen (e.g.: the hen was trained on red being palatable, and yellow being unpalatable, and the chicks were trained on red); (2) "opposite" where the chicks were trained on the hen's unpalatable food (e.g.: the hen was trained on red being palatable, and yellow being unpalatable, and the chicks were trained on yellow); (3) or "neither" when the hens were untrained (see Table 7.1).

Table 7.1: Combination of hens and chicks' training

| Training | Hen: Red (n=4) | Hen: Yellow (n=4) | Hen: Untrained (n=4) |
|---|---|---|---|
| Chicks: Red | Similar | Opposite | Neither |
| Chicks: Yellow | Opposite | Similar | Neither |

Prior to training, to identify the chicks belonging to the two groups within a brood, chicks were marked using two coloured stock markers (Blue and Green, Richey Sprayline, Richey Tagg Ltd, North Yorkshire, U.K.) on their neck or lower back. Each pair had a different coloured mark, and to identify chicks within the

pair, the location of the mark differed. The assignment of the chick group to the colour and order of conditioning and testing was counterbalanced between hens.

7.3.2.2 Conditioning

Once the hens were considered trained, the following day consisted of a conditioning phase, where chicks and hens were placed in two separate pens facing each other. A mesh wire separated the two pens allowing visual and auditory contact but not physical contact. For conditioning, the food was removed in the morning from the home pen 2:30 hours prior to the first session and replaced after the last session was finished. Consistent with the training regime which had three training sessions per day (late morning, early afternoon, late afternoon), the hen and the first pair of chicks were conditioned in the late morning session, and the hen and the second pair in the late afternoon session (see Table 7.2). In between the two conditioning sessions (early afternoon) the hen received another training session (where one feed was normal and the other was unpalatable), to control for some potential influence of the chick's behaviour on the hen, particularly if the chicks were trained on the opposite food colour to that of the hen. The order of the pair conditioning was counterbalanced across hens. The first pair of chicks was given plain food after their conditioning period rather than their trained colour so that they did not have any reinforcement towards their trained colour prior to the tests.

Table 7.2: Schedule example of a conditioning day

| | **Hen** | **Chicks – 1st Pair** | **Chicks – 2nd Pair** |
|---|---|---|---|
| **8:00** Remove food from home pen | | | |
| **T1: 10:30-11:00** | Conditioning with 1st pair | Conditioning | Fed on their trained colour |
| **T2: 13:30-14:00** | Fed on both colour: one palatable and the other unpalatable | Plain | Fed on their trained colour |
| **T3: 16:30-17:00** | Conditioning with 2nd pair | Plain | Conditioning |
| **17:00** Replace food in home pen | | | |

The conditioning session lasted half an hour, and each pair of chicks was able to feed in the presence of the hen, and the hen to feed in the presence of the chicks. The behaviour of all three individuals was recorded throughout the session. During the first five minutes, the chicks were presented with the two coloured foods, allowing the hen to observe her chicks (see Fig. 7.1). During the next five minutes, the food was removed from the chicks, and given to the hen. This should allow the chicks to observe the hen's behaviour in the presence of food. The food was then removed from the hen and given back to the chicks for another five minutes, then given back to the hen, and then one last time to the chicks for five minutes each (see Table 7.3). The food alternated between the hen and chicks for the first five sets of five minutes. Finally, the food was given to both the hen and chicks at the same time for the last (sixth) set of five minutes (see Table 7.3).

Figure 7.1: Plan view on the apparatus during conditioning when chicks had access to food but not hens

Table 7.3: Schedule of the conditioning session

| Time (min) | Chicks | Hen |
|---|---|---|
| 0-5 | Food | No Food |
| 5-10 | No Food | Food |
| 10-15 | Food | No Food |
| 15-20 | No Food | Food |
| 20-25 | Food | No Food |
| 25-30 | Food | Food |

Chicks from untrained hens were trained similarly to chicks from trained hens. In the conditioning period all chicks were given the choice between the two coloured foods (one novel and the other familiar). This design allowed examination of the behaviour of chicks with untrained hens to test for neophobia and for the effect of the presence of a hen on the probability of approaching a novel stimulus.

#### 7.3.2.3 Testing colour preferences

On the day following the conditioning (C+24h), the chicks were tested in their pair on their food colour preference. They were given the two coloured foods, in a similar set up to the conditioning period, but with the hen absent. Both pairs were tested simultaneously in separate pens, during late morning.

The chicks' feeding preferences were also tested on C+48h, C+120h and C+240h. On testing days, food from the home pen was removed in the morning 2:30 hours prior to the test and replaced right after the colour preference test. On non-testing days, food was ad-libitum. If the maternal behaviour during conditioning had affected the chicks' behaviour, then comparing the food preference results of different days after conditioning would enable me to measure not only how stable the chicks' preferences are, but also how long lasting the hen's influence is.

### 7.3.3 Video analysis

As in the previous experiments, videos were watched using the software package VLC. During conditioning, time and duration of all behaviours of hens and chicks were recorded on Microsoft Excel (see Table 7.4). The number of pecks directed at the food or ground was also recorded.

Table 7.4: Behaviour recorded during conditioning

| | |
|---|---|
| Drinking | Pecking from the water bowl. |
| Fight | Only in chick – when individuals peck each other and display. |
| Food Pecking | Pecking directed at one of the food bowls. The colour of the food pecked at is recorded. |
| Grid Pecking | Pecking explicitly directed at the separation mesh wire. |
| Ground Pecking | Pecking directed at the ground where the shaved wood is. |
| Ground Scratching | Scratching – usually prior to pecking – either on the floor or on the bowl. |
| Pecking Other | Pecking directed towards another individual. |
| Preening | Includes pecks directed at oneself and sunbathing. |
| Standing | When nothing else is done. Also includes "sitting" because it is hard to distinguish sitting from standing position as the view from the camera is from the top. |
| Walking | Movement. |

During the colour preference tests, only pecking related behaviour were recorded (see Table 7.5). The number of pecks directed at the food or ground was also recorded.

Table 7.5: Behaviour recorded during colour preference tests

| | |
|---|---|
| Drinking | Pecking from the water bowl. |
| Food Pecking | Pecking directed at one of the food bowls – record the colour of the bowl. |
| Grid Pecking | Pecking explicitly directed at the separation grid. |
| Ground Pecking | Pecking directed at the ground where the shaved wood and wood bar is. |
| Pecking Other | Pecking directed towards another individual. |
| Out of Sight | When chicks were out of sight from the camera. |

### 7.3.4 Model explanation

#### 7.3.4.1 Hen conditioning

For the analysis of the hens' behaviour during conditioning I first tested whether the hens behaved as expected according to their training. Nicol and Pope (1996, p.767) found that hens "*increased the rate of ground pecking and scratching when they had no food available, and increased the rate of food pecking (although not food ingestion) when they were given food*". The analysis of the hens' behaviour during conditioning is based on all three behaviour patterns, and how they change with the type of food (opposite or similar) that the chicks

eat. In the analysis of hens' behaviour in the conditioning period, all models included a random effect for hens. Because the total duration for each behaviour was positively skewed, I log transformed the food pecking dependent variable because it was always >0, and empirically logit transformed the ground pecking, ground scratching, and ground pecking and scratching dependent variables because these latter variables contained zero values.

Regarding food pecking, I analysed the data over the whole conditioning session, by looking at the amount of food eaten, regardless of its type. This was done by analysing the amount of time spent pecking at food, the number of pecks given at food sources, and the pecking rate. First, food pecking behaviour was analysed according to the proportion of food chicks were eating that was the opposite to the one that the hen was trained on ("opposite" food). Because untrained hens could not have chicks feeding on "opposite" food, the data were transformed so that chicks from untrained hens had a value of zero for this variable, and I then added whether the hen was trained or untrained as a second predictor variable. Thus a single coefficient was fitted for the duration of pecking in untrained hens, whereas for trained hens an intercept and slope (of the relationship with 'proportion opposite') was fitted. Those two predictor variables ('proportion opposite' and trained/untrained) were the main interest, but I also wanted to see if other variables could predict the hens' behaviour. Hence, in a second model, I also added the age of the chicks during conditioning, to look at whether hens would behave differently at different stages of the chicks' development; as well as the amount of food pecking done by the chicks, to see if the activity level of chicks would influence the hens' behaviour, as predictor variables.

Following Nicol and Pope's (1996) findings, I then analysed the hens' ground pecking and ground scratching behaviour across the three sets of five minutes when the hen had no access to food, but the chicks did (see Table 7.3). This was to look at immediate responses to the chicks. It was not possible to do the same for food pecking because during five of the six sets of five minutes, the hens could not food peck at the same time as the chicks. I first fitted a model with

only the proportion of time chicks spent feeding on opposite food and whether the hen was trained or untrained as predictor variables, as well as a second model that also included the age of the chicks and the amount of food pecking from the chicks.

#### 7.3.4.2 Comparing the estimates obtained to those of Nicol and Pope (1996)

To compare the results of the hens' behaviour to Nicol and Pope (1996), the differences between hens' behaviour when faced with chicks trained on "opposite" food and the behaviour of hens when faced with chicks trained on "similar" food were compared. Only trained hens were selected as Nicol and Pope (1996) did not have untrained hens in their experiment. For food pecking only the three five-minute sets where the hens had food (chicks had no food in the two first ones, but had food in the last one) were selected. For ground pecking and scratching the three sets of five minutes where the hen had no food and the chicks had food were selected. This is similar to Nicol and Pope's (1996) study. The 95% confidence interval of the mean difference between a hen faced with chicks trained on opposite food and a hen faced with chicks trained on similar food are reported for both the present study and the study conducted by Nicol and Pope (1996), allowing me to assess whether the findings are consistent.

#### 7.3.4.3 Chick conditioning

##### *7.3.4.3.1 Chick training*

First, I examined whether the chicks behaved according to their training: whether chicks trained on pecking at red pecked at a higher proportion towards red when yellow food was also present. I did not expect their preference to be as strong as the hens' because the chicks were not trained to find one colour palatable and the other unpalatable but simply to be familiar with one colour, the other one being novel at the time of the conditioning.

The chicks' behaviour was examined both during the first 5 minutes of the test, where the hens' had had the least opportunity in influencing their behaviour, as well as over all the conditioning period. The data were not normally distributed but the variance was homogenous (First five minutes: $F(1,42) = 0.59$; $p = 0.445$; Conditioning session: $F(1,42) = 1.08$; $p = 0.304$) so a Wilcoxon rank-sum test was used in both cases.

#### *7.3.4.3.2 Analysis of chicks' pecking behaviour based on the hen's pecking behaviour*

Chicks' foraging choices were then analysed to examine whether they were influenced by the hens' foraging choices and the behaviours Nicol and Pope (1996) reported.

First, to examine whether the chicks' choices were influenced by the hens' choices the proportion of coloured food chicks ate that was consistent with their training was analysed given the proportion of food a hen ate that was consistent with the chicks training, as well as whether the hens were trained or untrained. Looking at the pecking behaviour of the chicks relative to their training allows all hens (untrained and trained) to be included, and adding whether or not the hen was trained as a variable in the model allows looking for an effect of the hens' training. As above, a single coefficient was fitted for chicks exposed to untrained hens, whereas for those exposed to trained hens an intercept and slope (of the relationship with 'proportion food hen ate consistent with chick training') was fitted. The hens in this experiment pecked a lot more towards the unpalatable food than in Nicol and Pope's (1996) experiment, where hens directed fewer than 1 in 1000 pecks towards the unpalatable food. Hence instead of using a categorical variable of the food the hen was trained on to test for an effect of hen behaviour, I use a continuous variable that measures the proportion of time hens spent pecking at the food consistent with the chicks' training, which in our experiment better reflects the hens' behaviour. Similar models were fitted with the number of pecks and pecking rate as dependent variables, instead of the time spent pecking.

Because the dependent variable was a continuous variable bound between zero and one, an empirical logistic transformation was performed on the proportion of consistent food eaten by chicks, and nested random effects for pairs within hens were added to all models.

#### *7.3.4.3.3 Analysis of chicks' pecking behaviour based on Nicol and Pope's (1996) behaviour*

I analysed whether food pecking, ground pecking and ground scratching could predict the similarity of the hens' and chicks' pecking behaviour. To do this I calculated the difference of proportion of time spent by chicks and hens pecking on red food. This difference ranged from -1 to 1, so by taking the absolute value of this difference, both -1 and 1 are be indicative of a big difference and zero of no difference. I then subtracted the magnitude of this difference to one to have a measure of similarity. Because the similarity value was bound between zero and one, I empirically log transformed it. I then created a linear model (LM) with similarity as the dependent variable and total duration of food pecking, ground pecking and ground scratching as predictors. Nested random effects for pairs within hens were included. The results are shown in the Appendix 7.A

### 7.3.4.4 Finer analysis of the conditioning session

Because a weak correlation was found between the proportion of food eaten by the chick that was consistent with its training ("consistent food"), and the proportion of food eaten by the hen that was consistent with the chicks' training, the data were further analysed on a finer scale. This was to ascertain the direction of behavioural influence. Instead of running the models on the individual's behaviour on the whole conditioning session, the data were broken down into the five-minute subsets. To investigate the relationship between the chicks' and hens' foraging decisions, I first fitted models looking at the proportion of consistent food eaten by chicks during the 3$^{rd}$ and 5$^{th}$ five minute period, and had the hens' proportion of consistent food eaten during five minute periods preceding the chicks (2$^{nd}$ and 4$^{th}$ five minute periods) as a predictor variable. The five-minute period (3$^{rd}$ or 5$^{th}$) in which the behaviours were

recorded and the initial proportion of consistent food that chicks ate (during the 1st five minute period) were also added as predictor variables. Random effects were added for chicks. Second, I fitted models looking at the proportion of consistent food eaten by hens during the 2nd and 4th five minute periods, and had the chicks' proportion of consistent food eaten during the five minute periods preceding the hens as a predictor variable (1st and 3rd five minute periods). The data from the 6th period was not included in this finer analysis, because both hens and chicks had access to food during that time. Hence it would not be possible to separate the immediate behavioural effects from the ones of the previous five-minute period. The five-minute period and the proportion of consistent food that hens ate during the first five minutes (starting from the first peck) of training were also added as predictor variables. Random effects were added for hens.

#### 7.3.4.5 Chick colour preference

In order to investigate Caro and Hauser's (1992) third criterion, I needed to look at whether the transmission of information between the hen and her chicks lasted in absence of the hen. Therefore, the main question here was whether chicks preferentially ate the food colour that had been demonstrated to them by the hen during the conditioning period, at later periods in time. For this the proportion of time chicks spent pecking at the coloured food, consistent with the chicks' training, during the test phase was analysed given the proportion of time hens spent pecking at the coloured food, that was consistent with the chicks' training, during the conditioning period, as well as the test number (from one to four) were used as predictor variables. I first tested for an interaction between the two predictor variables, but given that it was not significant, I then analysed the main effects.

Because the dependent variable was a continuous variable bound between zero and one, an empirical logistic transformation was performed on the proportion of consistent food eaten by chicks during the test periods, and

random effects for hens were added to all models. ANOVA on the model was also used to look at the overall effect of the variables and interaction.

I also wished to test whether any effect of the hens' behaviour during conditioning on the chicks' behaviour during testing was mediated by the chicks' behaviour during conditioning. i.e. was any effect of the hen's behaviour during conditioning a result of immediate effects on chick behaviour that persisted until testing? To test this, a model (Model A) was fitted including only the effect of hens' behaviour on chicks' behaviour during testing, while a second model (Model B) was fitted including both the effect of hens' and chicks' behaviour during conditioning. If there was an effect of the hen's behaviour during conditioning that was wholly mediated through its immediate effect on chick behaviour, then I would expect an effect of hen behaviour in Model A, but not in Model B, with an effect of chick behaviour during conditioning in Model B (Shipley, 2000). Model B did not have residuals that were normally distributed ($W = 0.97$; $p = 0.001$). An appropriate transformation could not be found, meaning only strongly significant results should be taken as good evidence.

After analysing the proportion of time spent feeding by chicks on the food colour consistent with their training, similar analyses were fitted using the proportion of pecks and the pecking rate to the colour consistent with the chicks' training as indicators of food preference. In all cases I tested for an interaction first, then main effects where the interaction was non-significant ($p > 0.05$). I then repeated the mediation analysis described above for these dependent variables.

## 7.4 Results

### 7.4.1 Hen training

Eight hens were trained to prefer one colour over the other (four red, four yellow). Only one hen did not pass the criteria. Hence seven out of eight trained hens were included in the analysis. Although seven hens reached the training criterion, there were some difficulties during the training. The number of training trials required for each hen varied between three to twelve days, with a mean of 6.14 days.

Three of the four untrained hens had strong preferences (>87% of time or pecks directed at one colour). Out of those three hens, two had a strong preference for the red coloured food, and one for the yellow coloured food. The other hen had a milder preference (>65-75% for time and number of pecks respectively) for the yellow coloured food. From the untrained hens' behaviour, although there are strong individual preferences, there seem to be no overall preferences when looking across the sample of the population.

### 7.4.2 Hen conditioning

To verify if the hens behaved as expected following their training, I conducted a one-way independent analysis of variance looking at how the training affected the amount of red food being eaten by the hen during the conditioning period. There was a nearly significant effect of training on the amount of time spent pecking at red ($F(2,19) = 2.52$, $p = 0.107$). The effect sizes between the hens trained on red and the untrained hens, and between the hens trained on yellow and the untrained hens were small ($\omega = .36$, 95% C.I. = -0.28, 0.77 and $\omega = .12$, 95% C.I. = -0.44, 0.62 respectively), and the effect size between hens trained on red and hens trained on yellow was larger ($\omega = .58$, 95% C.I. = 0, 0.86). A similar analysis was conducted on the proportion of time spent eating red food. There was no significant effect of training on the proportion of red food eaten ($F(2,19) = 2.12$, $p = 0.148$). The effect sizes between the hens trained on red and the untrained hens, and between the hens trained on yellow and the

untrained hens were small ($\omega$ = .39, 95% C.I. = -0.24, 0.79 and $\omega$ = .04, 95% C.I. = -0.51, 0.56 respectively), and the effect size between hens trained on red and hens trained on yellow was larger ($\omega$ = .50, 95% C.I. = -0.11, 0.83).

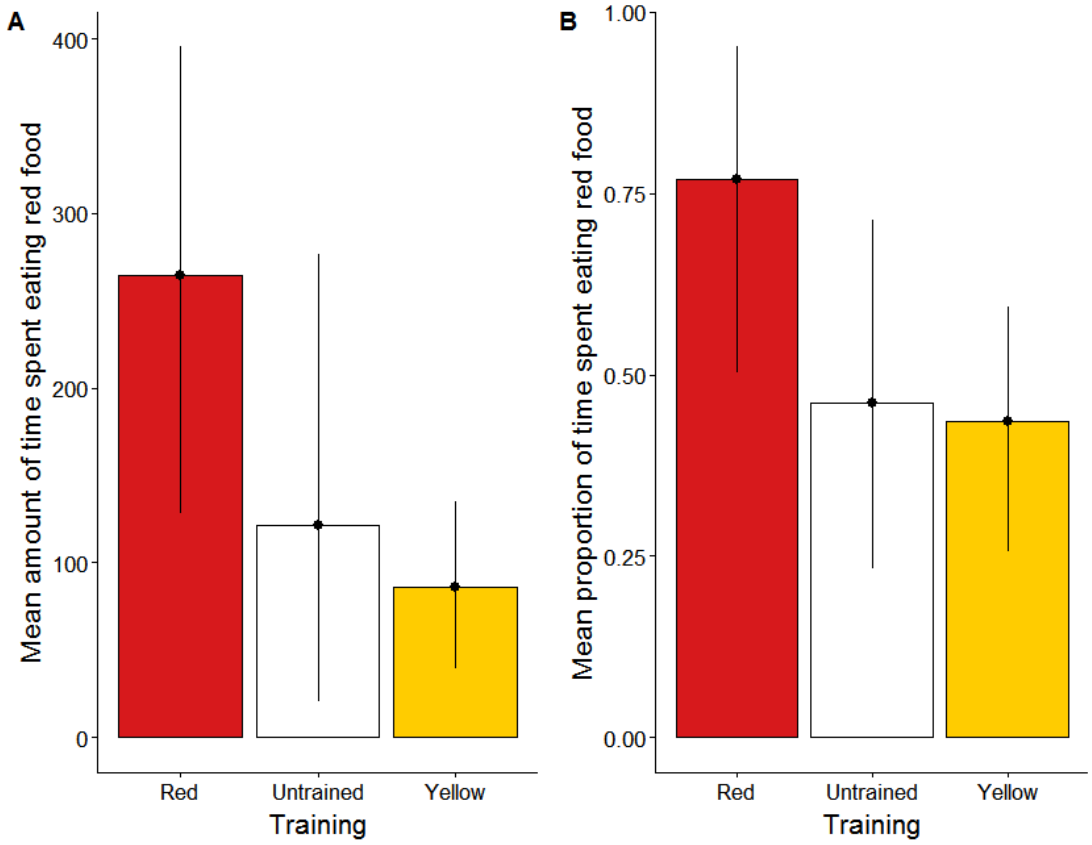


Figure 7.2: A) Mean amount and B) mean proportion of time hens pecked at red food by their training regime. Error bars are 95% C.I., not assuming normality

Although no significance of the effect of training on the eating behaviour was found, from Figure 7.2 A & B, it can be seen that hens trained on red ate more red food than untrained hens and hens trained on yellow. However training does not seem to be a particularly good predictor of hen's foraging behaviour. This is why for the further analysis, particularly modelling of the chick's behaviour, instead of using the training of hens as a proxy, their foraging behaviour was directly used, independent of their training.

#### 7.4.2.1 Food pecking behaviour

When including only *the proportion of time feeding on opposite food by chicks* and whether the hen was *trained* or *untrained*, there was no evidence of a difference between *trained* and *untrained* hens in their total time spent pecking (t = 1.20, d.f. = 9, p = 0.261). For trained hens, there was no evidence that the *total time spent pecking* was influenced by the *proportion of food chicks ate* that differed from the food the hens were trained on (t = -0.66, d.f. = 10, p = 0.523; see Fig. 7.3 and Table 7.6).

Table 7.6: Summary of linear mixed model estimating the *amount of time spent food pecking by the hen*, given the *proportion of time feeding on opposite food* by the chicks and whether or not the hen was *trained*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | 4.80 | 0.34 | 4.13, 5.47 | 10 | 14.1 | 0.000 |
| Proportion Opposite Chick | -0.26 | 0.39 | -1.02, 0.50 | 10 | -0.66 | 0.523 |
| Hen Trained (c.f. Untrained baseline) | 0.56 | 0.46 | -0.34, 1.46 | 9 | 1.20 | 0.261 |

Similar effects were found for the number of pecks (*proportion of pecks on opposite food by chicks* (t = -0.68; p = 0.511); *trained or untrained hen* (t = 1.06; p = 0.317)) and for pecking rate (*pecking rate on opposite food by chick* (t = 0.80; p = 0.441); *trained or untrained hen* (t = -1.25; p = 0.245)).

When also including *age* of the chicks and the amount of food pecking by the chicks, there was no evidence of a difference between *trained and untrained hens* (t = 1.27, d.f. = 8, p = 0.240). For trained hens, there was no evidence that the *total time spent pecking* was influenced by *the proportion of food a chick ate* that differed from the food the hens were trained on (t =-0.45, d.f. = 9, p = 0.664; see Fig. 7.3 and Table 7.7), the *age* of chicks at conditioning (t =-0.68, d.f. = 8, p = 0.514) or the *amount of food pecking by chicks* (t =0.02, d.f. = 9, p = 0.980).

Table 7.7: Summary of linear mixed model estimating the *amount of time spent food pecking by the hen*, given the *proportion of time feeding on opposite food by the chicks,* whether or not the hen was *trained*, the *age* of the chicks at conditioning and the overall *amount of food pecking by the chicks*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | 5.28 | 0.76 | 3.79, 6.77 | 9 | 6.91 | 0.0001 |
| Proportion Opposite Chick | -0.19 | 0.43 | -1.03, 0.65 | 9 | -0.45 | 0.665 |
| Hen Trained (c.f. Untrained baseline) | 0.63 | 0.50 | -0.35, 1.61 | 8 | 1.27 | 0.240 |
| Age Conditioning | -0.06 | 0.09 | -0.24, 0.12 | 8 | -0.68 | 0.514 |
| Food Pecking Duration Chick | 0.00001 | 0.0004 | -0.001, 0.001 | 9 | 0.03 | 0.980 |

Similar effects were found for the number of pecks (*proportion of pecks on opposite food by chicks* (t = -0.54; p = 0.603); *trained or untrained hen* (t = 1.04; p = 0.330); *age of chicks at conditioning* (t = -0.32; p = 0.759); *amount of pecks by chicks* (t = 0.14; p = 0.892)) and for pecking rate (*pecking rate on opposite food by chic*k (t = -0.88; p = 0.404); *trained or untrained hen* (t = -1.09; p = 0.306) *age of chicks at conditioning* (t = 1.09; p = 0.309); *rate of pecking by chicks* (t = 4.11; p = 0.003)). Here the overall pecking rate of chicks was positively correlated with the hens' pecking rate.

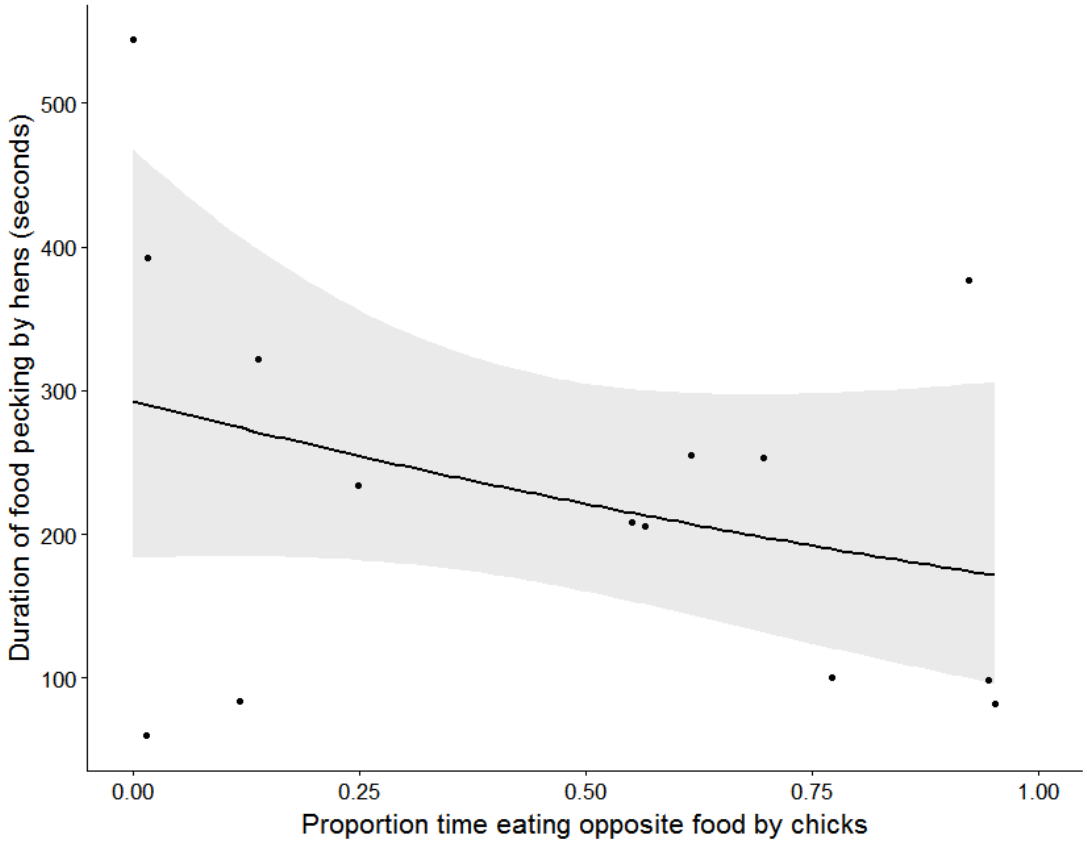


Figure 7.3: Duration of food pecking by trained hens (n=7) in seconds given the proportion of time chicks food peck at the opposite colour. The line is a fitted glm model with the quasi-Poisson family. The shaded band is the 95% C.I. on the fitted values. The slope is in the opposite direction to the prediction

#### 7.4.2.2 Ground pecking and ground scratching behaviour

When including only *proportion of time feeding on opposite food by chicks* and whether the hen was *trained* or *untrained*, there was no evidence of a difference between *trained* and *untrained* hens in *ground pecking and scratching* (t = -1.33, d.f. = 9, p = 0.215). For *trained* hens, there was no evidence that the *total time spent ground pecking plus ground scratching* was influenced by *the proportion of food a chick ate that differed from the food the hens were trained on* (t = 1.33, d.f. = 54, p = 0.188; see Fig. 7.4 and Table 7.8).

Table 7.8: Summary of linear mixed model estimating *the amount of time spent ground pecking and scratching by the hen*, given the *proportion of time feeding on opposite food by the chicks* and whether or not the hen was *trained*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -1.28 | 0.69 | -2.63, 0.07 | 54 | -1.86 | 0.068 |
| Proportion Opposite Chick | 1.03 | 0.77 | -0.48, 2.54 | 54 | 1.33 | 0.188 |
| Hen Trained (c.f. Untrained baseline) | -1.26 | 0.94 | -3.10, 0.58 | 9 | -1.33 | 0.215 |

Similar effects were found for the number of pecks (*proportion of pecks on opposite food by chicks* (t = 1.49; p = 0.068); *trained or untrained hen* (t = -1.38; p = 0.201)) and for pecking rate (*pecking rate on opposite food by chick* (t = 1.41; p = 0.164); *trained or untrained hen* (t = -1.43; p = 0.188)).

When I added the *age* of the chicks and the amount of food pecking from the chicks, I used a GLS model, with variance weighted by the *amount of food pecking by the chicks*, to allow for heteroscedasticity. There was no evidence of a difference between *trained and untrained hens* in *ground pecking and scratching* (t = -1.83, d.f. = 8, p = 0.105). For *trained* hens, there was weak evidence that the *total time spent ground pecking plus ground scratchin*g was influenced by the *proportion of food a chick ate that differed from the food the hens were trained on* (t = 1.72, d.f. = 53, p = 0.091; see Fig. 7.4). Hence, the more chicks seemingly made foraging errors, the more hens displayed their ground pecking and scratching when they do not have food. This is in line with what Nicol and Pope (1996) found. There was also evidence for a significant effect of the *amount of time spent food pecking by the chick* on the *amount of ground pecking and scratching by the hen* (t = -2.07, d.f. = 53, p = 0.044; see Table 7.9). The less a chick fed (whatever food colour it was), the more the hen displayed ground pecking and scratching when the hen had no access to food. Hence the hens' display is weakly adjusted to the proportion of time chicks feed on seemingly unpalatable food (as it would expected given a teaching function), but more importantly, the ground pecking and scratching displays increase as chicks feed less.

Table 7.9: Summary of linear mixed model estimating the *amount of time spent ground pecking and scratching by the hen*, given the *proportion of time feeding on opposite food by the chicks*, whether or not the hen was *trained*, the *age* of the chicks at conditioning and the overall *amount of food pecking by the chicks*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -1.09 | 1.37 | -3.78, 1.60 | 53 | -0.79 | 0.431 |
| Proportion Opposite Chick | 1.19 | 0.69 | -0.16, 2.54 | 53 | 1.72 | 0.091 |
| Hen Trained (c.f. Untrained baseline) | -1.60 | 0.87 | -3.31, 0.11 | 8 | -1.8 | 0.105 |
| **Food Pecking Duration Chick** | **-0.003** | **0.002** | **-0.01, -0.0002** | **53** | **-2.07** | **0.044 *** |
| Age Conditioning | 0.05 | 0.16 | -0.26, 0.36 | 8 | 0.28 | 0.788 |

The weak effect of *proportion of time spent food pecking on opposite food by chicks* in the model with *time spent food pecking by chicks* and *age of chicks at conditioning*, but the lack of an effect in the model without *time spent food pecking by chicks* and *age of chicks at conditioning* could be explained by the correlation (0.48) between the two predictors.

Similar effects were found for the number of pecks (*proportion of pecks on opposite food by chicks* (t = 1.70; p = 0.095); *trained or untrained hen* (t = -1.88; p = 0.097); *age of chicks at conditioning* (t = 0.37; p = 0.721); *amount of pecks by chicks* (t = -1.88; p = 0.062)) and for pecking rate (*pecking rate on opposite food by chick* (t = 1.80; p = 0.078); *trained or untrained hen* (t = -1.56; p = 0.158); *age of chicks at conditioning* (t = 0.03; p = 0.977); *rate of pecking by chicks* (t = -1.72; p = 0.092)).

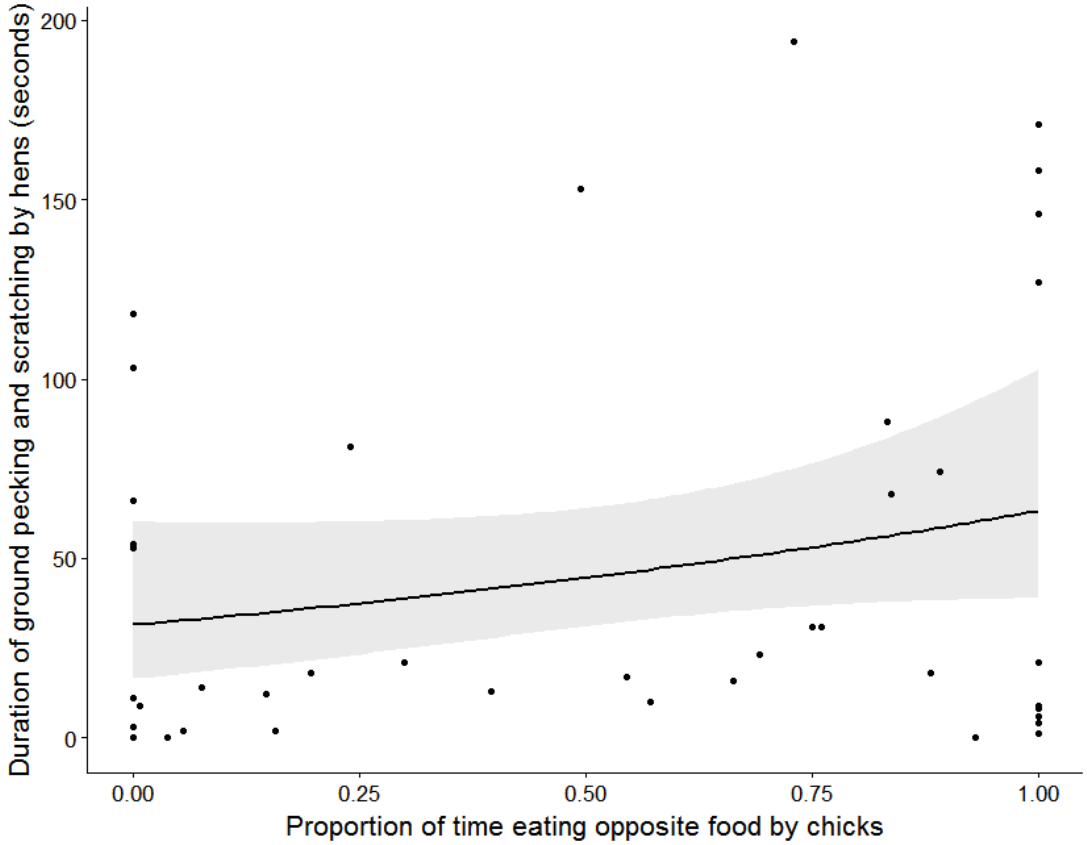


Figure 7.4: *Duration of ground pecking and ground scratching by trained hens* (n=7) in seconds given the *proportion of time chicks food peck at the opposite colour*. Figure includes the three sets of five minutes where the hen has no food and the chicks have food. The line is a fitted glm model with the quasi-Poisson family. The shaded band is the 95% C.I. on the fitted values

### 7.4.3 Comparing the estimates obtained to that of Nicol and Pope (1996)

In contrast with Nicol and Pope's (1996) findings, there was no strong evidence for hens modifying their behaviour when watching chicks feed on seemingly unpalatable food. However, there was a large overlap in 95% confidence intervals so there was little evidence that the pattern of results obtained are statistically inconsistent with Nicol and Pope's (1996) findings (see Table 7.10). The 95% confidence intervals for this study span zero, meaning that the difference between the hens' behaviour when faced with chicks trained on opposite food and chicks trained on similar food, is non-significant at the 5% level.

Table 7.10: 95% confidence intervals of the difference of hens' behaviour when faced with chicks trained on opposite food and chicks trained on similar food

| 95% Confidence Intervals | Nicol and Pope (1996) | This Study |
|---|---|---|
| Food Pecking | 22.1, 243 | -61.9, 67.4 |
| Ground Pecking & Scratching | 3.49, 147 | -4.36, 60.0 |

### 7.4.4 Chick conditioning

#### 7.4.4.1 Chick training

During the first five minutes, the *proportion of red food eaten* by chicks trained on red (Mdn = 0.59) did not differ significantly from chicks trained on yellow (Mdn = 0.22), W = 270, p = 0.511. The effect size was small (r = .12, 95% C.I. = -0.19, 0.41). During the whole session the *proportion of red food eaten* by chicks trained on red (Mdn = 0.78) was significantly bigger than that of chicks trained on yellow (Mdn = 0.12), W = 360, p = 0.006 (Fig 7.5). It did represent a medium-sized effect (r = .47, 95% C.I. = 0.2, 0.83). The difference observed between the analysis of the whole session and the first five minutes could be due to a lack of power in the latter case.

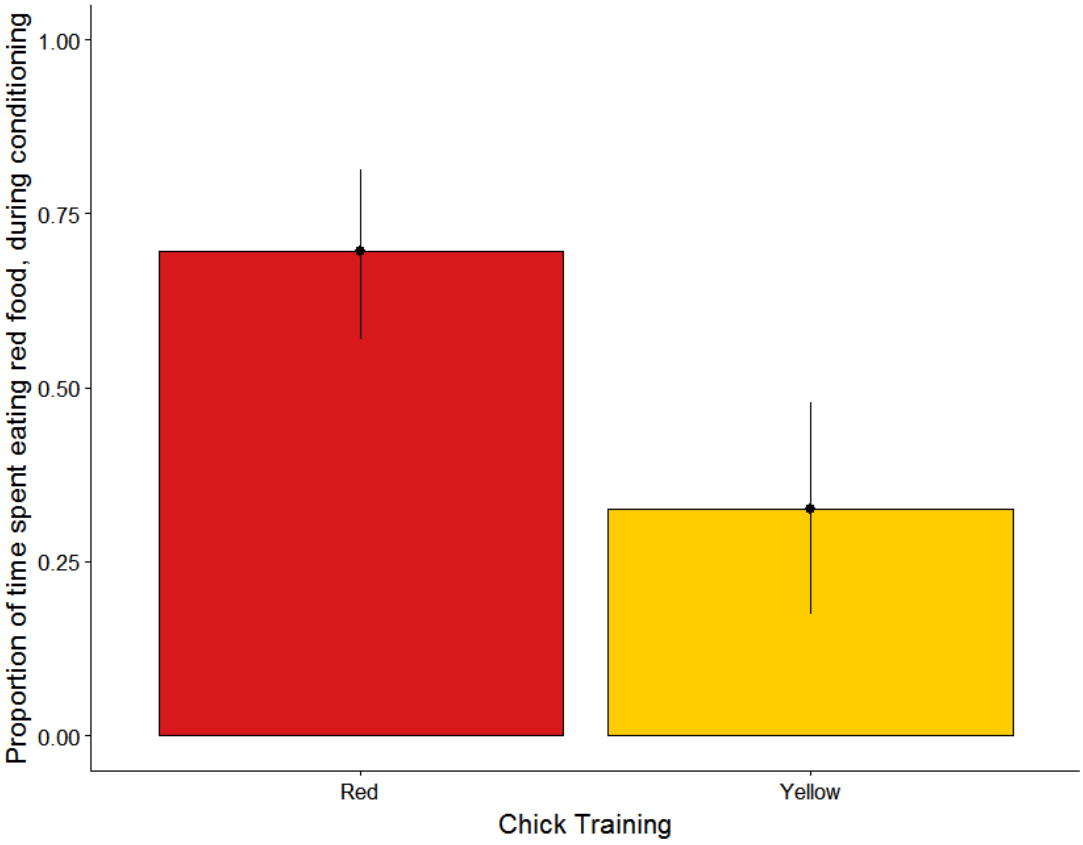


Figure 7.5: *Proportion of time spent pecking at red food*, during the whole conditioning session, according to the chick's training. Error bars are 95% C.I., not assuming normality

#### 7.4.4.2 Analysis of chicks' pecking behaviour based on the hen's pecking behaviour

When including the *proportion of time spent feeding by hens on food consistent with the chicks' training*, the hens' *training* and the interaction between the two, a GLS model was used, with variance weighed by the *proportion of consistent food being pecked at by the hen*, to allow for heteroscedasticity. There was no evidence of an interaction (t = 0.59, d.f. = 31, p = 0.571, see Table 7.11), therefore the interaction was dropped in the next model.

Table 7.11: Summary of the linear mixed model fitting *the proportion of food consistent with the chicks' training by the chicks* given the interaction between the *proportion of food consistent with the chicks' training by the hens* and the hens' *training*

| Variable | Estimate | Std Error | 95% C.I | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | 0.10 | 1.00 | -1.86, 2.06 | 22 | 0.10 | 0.924 |
| Hen Proportion Consistent Chick Training | 1.93 | 1.60 | -1.21, 5.07 | 9 | 1.28 | 0.232 |
| Hen Trained (c.f. Untrained baseline) | -1.63 | 1.70 | -4.96, 1.70 | 9 | -0.96 | 0.365 |
| Hen Proportion : Hen Training | 1.40 | 2.38 | -3.26, 6.06 | 9 | 0.59 | 0.571 |

Similar effects were found for the number of pecks (*proportion of pecks made by the hen towards the food consistent with the chicks' training* (t = 1.17; p = 0.272); *trained or untrained hen* (t = -1.24; p = 0.247); interaction (t = 0.77; p = 0.461)) and for pecking rate (*pecking rate of hen towards food that is consistent with the chicks' training* (t = 4.53; p = 0.001); *trained or untrained hen* (t = -0.22; p = 0.834); interaction (t = -0.55; p = 0.593)).

When including only the main effects, a GLS model was used, with variance weighed by the *proportion of consistent food being pecked at by the hen,* to allow for heteroscedasticity. There was no evidence of a difference between *trained and untrained hens* (t = -0.97, d.f. = 9, p = 0.358). For *trained* hens, there was weak evidence that the *proportion of time a chick spent pecking at the coloured food that was consistent with the chicks' training* was positively influenced by the

*proportion of time hens spent pecking at the coloured food that was consistent with the chicks' training* (t = 2.18, d.f. = 10, p = 0.055; see Fig. 7.6 and Table 7.12).

Table 7.12: Summary of the linear mixed model fitting the *proportion of food consistent with the chicks' training by the chicks* given the *proportion of food consistent with the chicks' training by the hens* and the hens' *training*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -0.24 | 0.82 | -1.85, 1.37 | 22 | -0.29 | 0.775 |
| Hen Proportion Consistent Chick Training | 2.49 | 1.15 | 0.24, 4.74 | 10 | 2.18 | 0.055 |
| Hen Trained (c.f. Untrained baseline) | -0.73 | 0.75 | -2.20, 0.74 | 9 | -0.97 | 0.358 |

I found similar effects for number of pecks (*proportion of pecks made by the hen towards the food consistent with the chicks' training* (t = 2.16; p = 0.056); *trained or untrained hen* (t = -1.09; p = 0.264)) and for pecking rate (*pecking rate of hen towards food that is consistent with the chicks' training* (t = 4.70; p = 0.001); *trained or untrained hen* (t = -2.43; p = 0.038)).

Because there was no evidence of an effect of the hens' *training*, only the hens' behaviour was included in the final model. A GLS model was used, with variance weighed by the *proportion of consistent food being pecked at by the hen*, to allow for heteroscedasticity. There was weak evidence that the *proportion of time a chick spent pecking at the coloured food that was consistent with the chicks' training* was influenced by the *proportion of time hens spent pecking at the coloured food that was consistent with the chicks' training* (t = 2.09, d.f. = 32, p = 0.063; see Fig. 7.6 and Table 7.13). The more time the hen spent pecking at the colour the chick was trained on, the more chicks spent time pecking at that colour.

Table 7.13: Summary of the linear mixed model fitting the *proportion of food consistent with the chicks' training by the chicks* given the *proportion of food consistent with the chicks' training by the hens*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -0.43 | 0.80 | -2.00, 1.14 | 22 | -0.53 | 0.600 |
| Hen Proportion Consistent Chick Training | 2.36 | 1.13 | 0.15, 4.57 | 10 | 2.09 | 0.063 |

Similar effects were found for the number of pecks (*proportion of pecks made by the hen towards the food consistent with the chicks' training* (t = 2.02; p = 0.071)), and for pecking rate (*pecking rate of hen towards food that is consistent with the chicks' training* (t = 4.27; p = 0.002)). In all cases, there was an effect of the pecking rate of the hen: the higher the pecking rate of the hen towards food that was consistent with the chicks' training, the higher the pecking rate of the chicks.

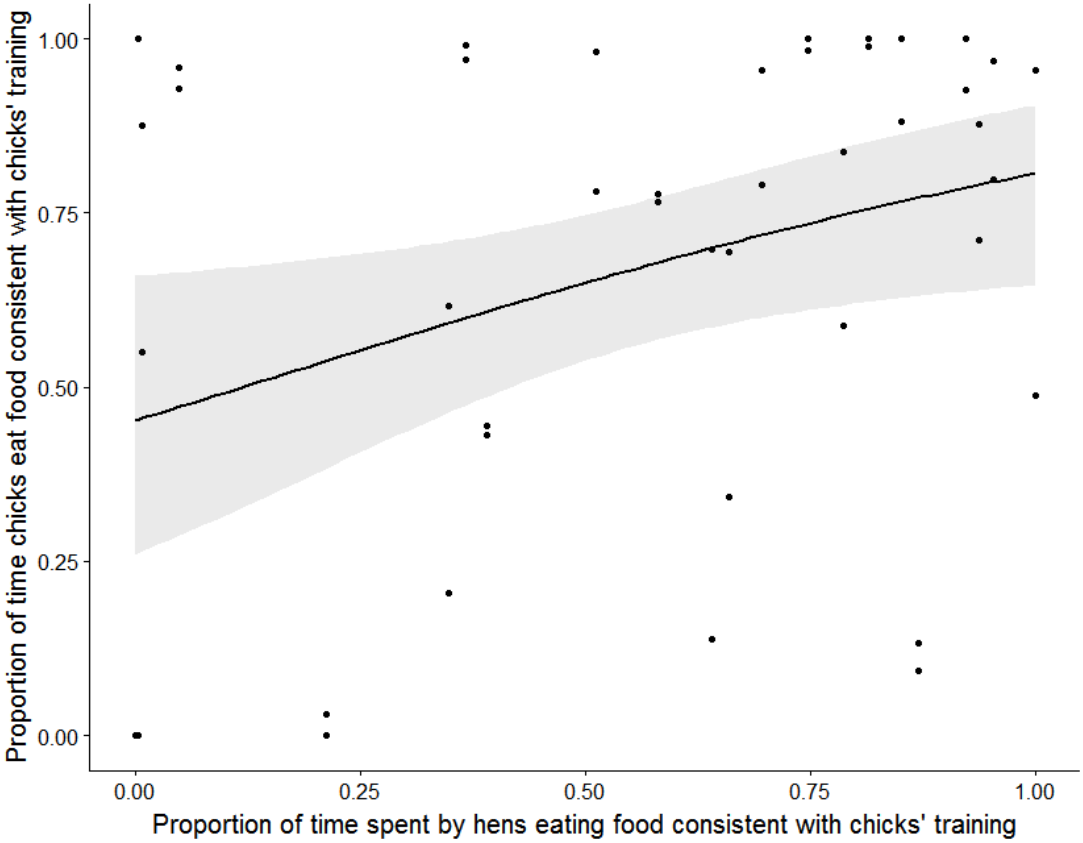


Figure 7.6: *Proportion of time spent by chicks eating food consistent with the chicks' training* (n=44) given the *proportion of time spent by hens eating food consistent with the chicks' training.* The line is a fitted glm model with the quasi-binomial family. The shaded band is the 95% C.I. on the fitted values

Further analyses were conducted on how the chicks' pecking behaviour was affected by the two behaviours reported in Nicol and Pope (1996): food pecking, ground pecking and ground scratching. However, because I did not see any effect of chicks feeding from opposite food on the hens' behaviour, the aforementioned analyses are reported in the appendix (7.A).

### 7.4.5 Finer analysis of the conditioning session

#### 7.4.5.1 Chicks' behaviour

When including the *proportion of time spent feeding by hens on food consistent with the chicks' training*, the *five-minute period* during conditioning from which the data are taken (a factor to allow for any difference between the two five-minute periods), the interaction between the two and *the initial proportion of time spent feeding by chicks on food consistent with their training*, there was no evidence of an effect of the interaction (t = 0.37, d.f. = 41, p = 0.711, see Table 7.14), therefore the interaction was dropped in the next model.

Table 7.14: Summary of linear mixed model estimating the *proportion of time spent pecking at consistent food by chicks*, given the *proportion of time spent pecking at consistent food by the hen*, the *initial proportion by chicks*, *time period* and interaction

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -1.09 | 0.74 | -2.54, 0.36 | 42 | -1.49 | 0.144 |
| Time (5th period) | -0.43 | 0.91 | -2.21, 1.35 | 41 | -0.47 | 0.638 |
| Previous Proportion Consistent Hen | 0.05 | 1.12 | -2.15, 2.25 | 41 | 0.05 | 0.965 |
| **Initial Proportion Consistent Chick (1st period)** | **2.55** | **0.71** | **1.16, 3.94** | **42** | **3.61** | **0.0008 ***** |
| Time (5th): Previous Proportion Consistent Hen | 0.53 | 1.43 | -2.27, 3.33 | 41 | 0.37 | 0.711 |

When fitting the model only with the main effects, there was no evidence that the *proportion of time spent pecking by chicks at the coloured food consistent with their training* was affected by the *five minute period* (t = -0.29, d.f. = 42, p = 0.770) or by *the proportion of time spent pecking by hens at the coloured food consistent with the chicks' training* (t = 0.54., d.f. = 42, p = 0.595). However there was an effect of the *proportion of time spent pecking by chicks at the coloured food consistent with their training* during the 1st five-minute period (t = 3.61, d.f. = 42, p = 0.001; see Table 7.15), suggesting that initial preferences carry through to later periods during conditioning.

Table 7.15: Summary of linear mixed model estimating the *proportion of time spent pecking at consistent food by chicks*, given the *proportion of time spent pecking at consistent food by the hen* and the *initial (1st period) proportion of time spent pecking at consistent food by chicks* and *time period*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -1.25 | 0.61 | -2.45, -0.05 | 42 | -2.04 | 0.047 |
| Time (5th) | -0.17 | 0.57 | -1.29, 0.95 | 42 | -0.29 | 0.770 |
| Proportion Cons Hen | 0.38 | 0.70 | -0.99, 1.75 | 42 | 0.54 | 0.595 |
| **Initial Proportion Cons Chick** | **2.52** | **0.70** | **1.15, 3.89** | **42** | **3.61** | **0.001** |

7.4.5.2 Hens' behaviour

When including the *proportion of time spent feeding by chicks on food consistent with their training*, the *five-minute period*, the interaction between the two and the *proportion of time spent feeding by hens on food consistent with the chicks training during the first five minutes of the hens' last training period*, there was no evidence of an effect of the interaction (t = -0.17, d.f. = 29, p = 0.870, see Table 7.16), therefore the interaction was dropped in the next model.

Table 7.16: Summary of linear mixed model estimating the *proportion of time spent pecking at consistent food by hens*, given the *proportion of time spent pecking at consistent food by the chicks*, the *five-minute period*, their interaction and the *proportion of time spent pecking at consistent food by hens during the first five minutes of their last training*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -2.35 | 1.36 | -5.02, 0.32 | 29 | -1.73 | 0.094 |
| Time (4th period) | -0.71 | 1.86 | -4.36, 2.94 | 29 | -0.38 | 0.705 |
| Previous Proportion Consistent Chick | 2.69 | 2.05 | -1.33, 6.71 | 29 | 1.31 | 0.199 |
| Training Proportion Consistent Hen | 2.30 | 1.21 | -0.07, 4.67 | 29 | 1.90 | 0.067 |
| Time (4th): Prev Prop Consistent Chick | -0.45 | 2.74 | -5.82, 4.92 | 29 | -0.17 | 0.870 |

When fitting the model only with the main effects, there was no evidence that the *proportion of time spent pecking by hens at the coloured food consistent with their training* was affected by the *five minute period* (t = -0.85, d.f. = 30, p = 0.403). There was however weak evidence that the *proportion of time spent pecking by chicks at the coloured food consistent with their training* (t = 1.81, d.f. =

30, p = 0.079) and the *proportion of time spent pecking by hens at the coloured food consistent with the chicks' training during the first five minutes of the hens' last training period* (t = 1.95, d.f. = 30, p = 0.060; see Table 7.17) had an effect on the *proportion of time spent pecking by hens at the coloured food consistent with the chicks' training*.

Table 7.17: Summary of linear mixed model estimating the *proportion of time spent pecking at consistent food by hens*, given the *proportion of time spent pecking at consistent food by the chicks*, the *five-minutes period* and the *proportion of time spent pecking at consistent food by hens during the first five minutes of their last training*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -2.24 | 1.16 | -4.51, 0.03 | 30 | -1.93 | 0.063 |
| Time ($4^{th}$) | -0.96 | 1.13 | -3.17, 1.25 | 30 | -0.85 | 0.403 |
| Proportion Consistent Chick | 2.44 | 1.34 | -0.18, 5.07 | 30 | 1.81 | 0.079 |
| Training Proportion Consistent Hen | 2.32 | 1.19 | -0.01, 4.65 | 30 | 1.95 | 0.060 |

### 7.4.6 Chick colour preferences

When including the *proportion of time spent feeding by hens on food consistent with the chicks' training*, the *test* number and interaction between the two, there was no evidence of an effect of the interaction (F = 1.65, d.f. = 126, p = 0.181, see Table 7.18 and 7.19), therefore the interaction was dropped in the next model.

Table 7.18: Summary of the linear mixed model fitting the *proportion of food eaten by the chicks that is consistent with their training* during the test period given the *proportion of food eaten by the hens that is consistent with the chicks' training during conditioning*, the *test* period and their interaction

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -0.51 | 1.25 | -2.96, 1.94 | 126 | -0.41 | 0.682 |
| Hen Proportion Consistent Chick Training During Conditioning | -0.15 | 1.92 | -3.91, 3.61 | 42 | -0.08 | 0.940 |
| **Test 2** | **-3.02** | **1.34** | **-5.65, -0.39** | **126** | **-2.26** | **0.026 *** |
| Test 3 | -1.67 | 1.34 | -4.30, 0.96 | 126 | -1.25 | 0.215 |
| Test 4 | -1.82 | 1.34 | -4.45, 0.81 | 126 | -1.36 | 0.175 |
| **Hen Proportion : Test 2** | **4.15** | **2.05** | **0.13, 8.17** | **126** | **2.02** | **0.045 *** |
| Hen Proportion: Test 3 | 2.00 | 2.05 | -2.02, 6.02 | 126 | 0.98 | 0.331 |
| Hen Proportion: Test 4 | 3.61 | 2.05 | -0.41, 7.63 | 126 | 1.76 | 0.081 |

Table 7.19: Anova of the linear mixed model fitting the *proportion of food eaten by the chicks that is consistent with their training during the test period* given the *proportion of food eaten by the hens that is consistent with the chicks' training during conditioning*, the *test* period and their interaction

| Variable | Num DF | Den DF | F-value | p-value |
|---|---|---|---|---|
| (Intercept) | 1 | 126 | 3.15 | 0.078 |
| Hen Prop Consistent Chick Training During Conditioning | 1 | 42 | 2.50 | 0.121 |
| Test | 3 | 126 | 0.80 | 0.497 |
| Hen Proportion : Test | 3 | 126 | 1.65 | 0.181 |

Similar effects were found for the number of pecks (*proportion of pecks by hens on coloured food consistent with the chicks' training* (F = 1.81; p = 0.185); *test* (F = 0.90; p = 0.445) and interaction (F = 1.35, p = 0.260)) and for pecking rate (*proportion of pecks by hens on coloured food consistent with the chicks' training* (F = 2.92; p=0.095); *test* (F = 1.20; p=0.311) and interaction (F = 0.24, p = 0.867)).

When fitting the model only with the main effects, there was no evidence that the *proportion of time spent pecking by chicks at the coloured food consistent with their training* was affected by the *test* (F = 0.78, d.f. = 129, p = 0.506; see Fig. 7.7)

or by the *proportion of time spent pecking by hens at the coloured food consistent with the chicks' training* (F = 2.54., d.f. = 42, p = 0.118; see Table 7.20 and 7.21).

Table 7.20: Summary of the linear mixed model fitting the *proportion of food eaten by the chicks that is consistent with their training during the test period* given the *proportion of food eaten by the hens that is consistent with the chicks' training during conditioning and the test period*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -1.88 | 1.03 | -3.90, 0.14 | 129 | -1.83 | 0.069 |
| Hen Proportion Consistent Chick Training During Conditioning | 2.29 | 1.44 | -0.53, 5.11 | 42 | 1.60 | 0.118 |
| Test 2 | -0.69 | 0.69 | -2.04, 0.66 | 129 | -1.01 | 0.314 |
| Test 3 | -0.54 | 0.69 | -1.89, 0.81 | 129 | -0.79 | 0.430 |
| Test 4 | 0.21 | 0.69 | -1.14, 1.56 | 129 | 0.30 | 0.765 |

Table 7.21: Anova of the linear mixed model fitting the *proportion of food eaten by the chicks that is consistent with their training during the test period* given the *proportion of food eaten by the hens that is consistent with the chicks' training during conditioning and the test period*

| Variable | Num DF | Den DF | F-value | p-value |
|---|---|---|---|---|
| (Intercept) | 1 | 129 | 3.20 | 0.076 |
| Hen Proportion Consistent Chick Training During Conditioning | 1 | 42 | 2.54 | 0.118 |
| Test | 3 | 129 | 0.78 | 0.506 |

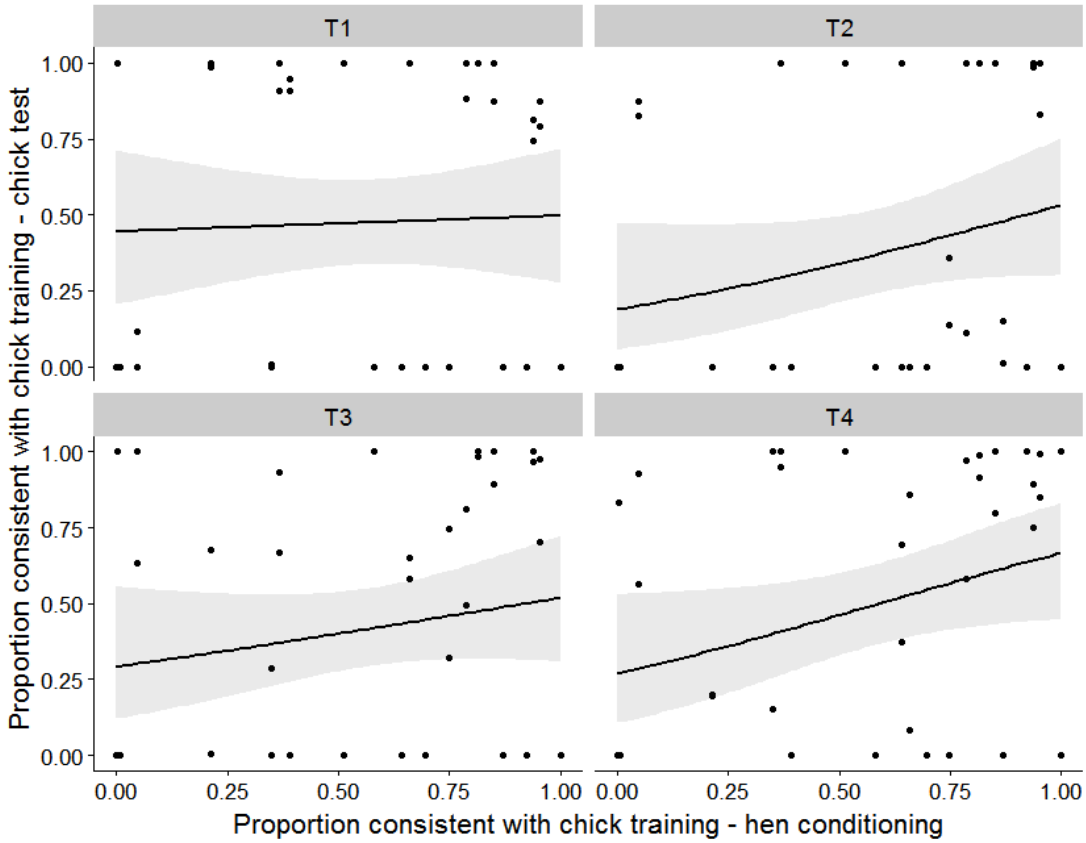


Figure 7.7: *Proportion of food eaten by chicks consistent with their training in the testing period* given the *proportion of food eaten by hens consistent with the chicks' training in the conditioning period*, according to the *test* period (T1: 24h post-conditioning; T2: 48h post-conditioning; T3: 120h post-conditioning; T4: 240h post-conditioning). The line is a fitted glm model with the quasi-binomial family. The shaded band is the 95% C.I. on the fitted values

Similar effects were found for the number of pecks (*proportion of pecks by hens on coloured food consistent with the chicks' training* (F = 1.85; p = 0.181) and *test* (F = 0.89; p = 0.451)) and for pecking rate (*proportion of pecks by hens on coloured food consistent with the chicks' training* (F = 2.96; p = 0.092) and *test* (F = 1.25; p = 0.296)).

A final analysis was conducted with only the hens' behaviour as a predictor variable. Because the results were similar to those with the hens' behaviour and the tests as predictor variables, the findings are reported in the appendix (7.B)

There was no evidence of a significant effect of the hen's foraging choice during conditioning on the chicks foraging choice during the tests. However I wanted to test for the teaching pathway to know whether the effect of the hens'

foraging choices during conditioning on the chicks' foraging choice during test are mediated by the chicks' foraging choices during conditioning. If the teaching pathway operates then I would expect the effect of the hen's behaviour to disappear when I add the chick's behaviour during conditioning (Shipley, 2000).

I therefore fitted a similar model to the previous one including the *proportion of time spent by chicks pecking at the coloured food consistent with their training during the conditioning period*. There was evidence that the *proportion of time spent pecking by chicks at the coloured food consistent with their training during the tests* was affected by the *proportion of time spent pecking by chicks at the coloured food consistent with their training during the conditioning period* (t = 3.19, d.f. = 41, p = 0.003; see Table 7.22)

Table 7.22: Summary of the linear mixed model fitting the *proportion of food eaten by the chicks that is consistent with their training during the test period* given the *proportion of food eaten by the hens that is consistent with the chicks' training during conditioning* and the *proportion of food eaten by the chicks that is consistent with the chicks' training during conditioning*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -4.06 | 1.03 | -6.08, -2.04 | 132 | -3.93 | 0.0001 |
| Hen Proportion Consistent Chick Training During Conditioning | 0.79 | 1.37 | -1.90, 3.48 | 41 | 0.58 | 0.567 |
| **Chick Proportion Consistent Chick Training During Conditioning** | **4.17** | **1.30** | **1.62, 6.72** | **41** | **3.19** | **0.003 **** |

The effects of the hens' foraging choice decreased when adding the chicks' foraging choice during conditioning (Table 7.22). When comparing the results of the model in Table 7.B.1 in the Appendix, it suggests that the *proportion of food hens ate that was consistent with the chicks' training during conditioning* predicted the *proportion of food chicks ate consistent with the chicks training during conditioning* (as found in 7.4.4.2), which in turns influenced the *proportion of food chicks ate consistent with the chicks' training during tests* (Fig. 7.8).

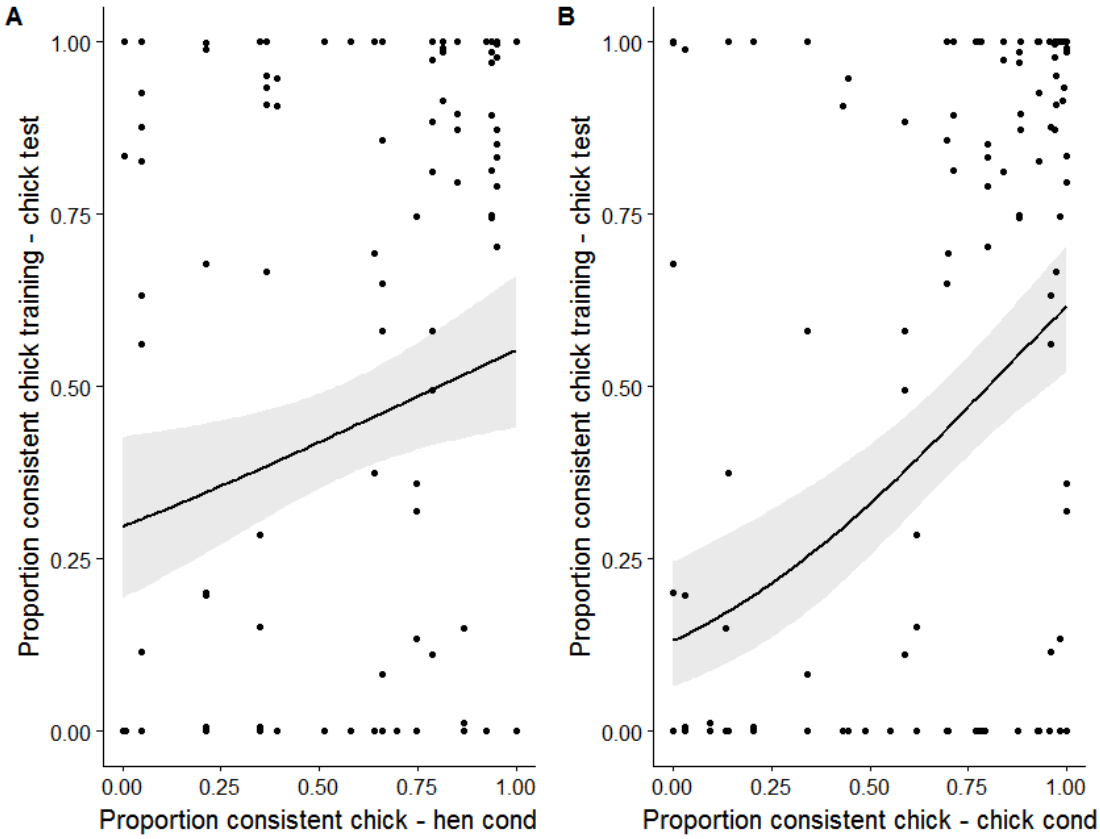


Figure 7.8: *Proportion of consistent food eaten by chicks during the testing periods* given A) *the proportion of consistent food eaten by hens during the conditioning period* and B) the *proportion of consistent food eaten by chicks during the conditioning period*. The line is a fitted glm model with the quasi-binomial family. The shaded band is the 95% C.I. on the fitted values

Similar effects were found for the number of pecks (*proportion of pecks by hens on coloured food consistent with the chicks' training* (t = 0.41; p = 0.684) and *proportion of pecks by chick on coloured food consistent with the chicks' training during conditioning* (t = 3.33; p = 0.002)) and for pecking rate (*proportion of pecks by hens on coloured food consistent with the chicks' training* (t = -0.54; p = 0.596) and *proportion of pecks by chick on coloured food consistent with the chicks' training during conditioning* (t = 5.45; p = 0.000)).

## 7.5 Discussion

The aim of this study was threefold: To 1) replicate Nicol and Pope's (1996) findings that hens increase their foraging display when chicks seemingly make a foraging error; 2) examine whether chicks alter their behaviour in response to the hens' display and start pecking predominantly at the seemingly correct food, and 3) assess how long their response lasts in absence of a reinforced demonstration.

### 7.5.1 Findings

#### 7.5.1.1 Hen's behaviour during conditioning

The hens in this experiment did not behave as expected: their *food pecking* behaviour did not increase with the *proportion of "opposite" food being eaten by the chicks*, and their *ground pecking and ground scratching* behaviour only weakly increased. This weak effect was however only found when the model included the age of chicks, the amount of food pecking by the chicks and the hens' training. The weak increase in display found only when hens had no food could be due to the fact that when hens had access to food, they might be too occupied to find out which food is palatable, which could lead them to pay less attention to the chicks' behaviour. On the other hand, when no food is present, the hens might pay more attention to their chicks and behave accordingly. Moreover, the *ground pecking and scratching* display increased as chicks fed less. This could potentially encourage chicks to look for food when they were not actively feeding. Similarly, Wauters and Richard-Yris (2002) found evidence that hens food call more when their chicks are not actively feeding prior to the food call emission. This suggests that hens might be able to modify the emission of vocalisation based on the chicks' behaviour. This reinforces Nicol and Pope's (1996) findings that hens were able to modify their gestural communication in relation the chick's behaviour. However, in my experiment, the increase of foraging display based on the chicks foraging activity was however not found when looking at the hens' *food pecking* behaviour.

Despite finding little evidence that hens modify their behaviour based on perceived errors of chicks, when comparing our results to Nicol and Pope's (1996), the 95% C.I. largely overlapped, suggesting that there was little evidence that the pattern of results obtained in this experiment were inconsistent with Nicol and Pope's (1996) findings, i.e. it is plausible the same effects are in operation, and that the result differed by chance. Therefore, my findings by themselves offer no strong reason to doubt Nicol and Pope's (1996) findings.

When looking at the five-minute periods where only chicks had food but hens did not, there was a negative but not significant relationship between the *training* of the hen and the *amount of ground pecking and ground scratching*: trained hens displayed less ground pecking and scratching. One possible explanation is that while the chicks were foraging, hens might be acquiring new but not necessarily conflicting information about the food. In fact, by the end of the training, hens showed a preference for one food (this was the criterion for training) but did not show a strong aversive reaction to the other food, despite doubling the quinine concentration that was used in Nicol and Pope's (1996) study. The lack of aversion towards the unpalatable food in this study signifies that the hens might not have acquired sufficient knowledge that one food was aversive, and therefore did not increase their display when confronted with chicks eating the "wrong" food. But while watching the chicks the hens could have received information about the quality of their non-preferred food, and hence they could be paying attention to the chicks' behaviour to incorporate socially acquired information about the food rather than displaying to the chicks that the food was aversive. On the other hand, untrained hens had sampled both foods fairly similarly during their training, and therefore were not receiving new information about the food.

#### 7.5.1.2 Chicks' behaviour during conditioning

There was some weak evidence of a correlation between the *proportion of food consistent with the chicks' training eaten by the chicks* and *that eaten by the hens when the conditioning period* was analysed overall. There was however little

evidence that the *food pecking*, *ground pecking and ground scratching behaviour of the hen* had an impact on the *similarity* between the chicks and hens' food choices. This could be explained by the fact that those three behavioural patterns did not increase in reaction to chicks seemingly making foraging errors.

When looking in further detail at the correlation between the hens and chicks' foraging choices, unexpectedly there was little evidence supporting a relationship between the *proportion of time spent by chicks pecking at food consistent with their training* and the *proportion of time spent by hens pecking at food consistent with the chicks' training* in the five-minute periods preceding the period where chicks had access to food. However there was weak evidence that the *proportion of time spent by hens pecking at food consistent with the chicks' training* was affected by the *proportion of time spent by chicks pecking at food consistent with their own training* in the five-minute periods preceding the period in which hens had access to food. Those findings suggest that while the chicks were not socially influenced by the hens' foraging choices, the hens might have been influenced by the choices of their chicks.

Moreover, the chicks' foraging choices during the several five-minute periods where they had access to food but the hens did not were highly consistent with the chicks' foraging choices during the first of those five-minute periods, where the chicks had had no prior demonstration from the hen. Similarly, but to a lesser extent, hens' foraging choices during the five-minute periods where they had food but the chicks did not were consistent with the hens' foraging choice during training. Hence, both chicks and hens appear somewhat conservative in their foraging decisions.

#### 7.5.1.3 Chicks' preferences during the colour preference tests

When looking at the chicks' foraging choices in the four colour preference tests where no hen was present, very weak evidence that the correlation between the hens' foraging choices during conditioning and the chicks' foraging

choices during the tests remained. This correlation was in large part mediated by the chicks' foraging choices during conditioning.

In this experiment chicks kept their arbitrary foraging preferences for at least 10 days. However, rather than the hens' foraging choices during conditioning affecting the chicks' foraging choices during conditioning, which in turn predicted the chicks' foraging choices during the tests, it seemed that the chicks' foraging choices during conditioning predicted both the hens' foraging choices during the conditioning period and the chicks' foraging choices during the test periods.

### 7.5.2 General points

#### 7.5.2.1 Limitations

Overall, there was a lot of individual variation in both hens' and chicks' behaviour. Other experiments have shown high individual variation. For instance, Wauters et al. (2002) found that the feeding activities of the hens and their food calling frequency varied significantly between individuals, and Sherwin et al. (2002) found that hens' reaction to the demonstration of disgust behaviour also varied significantly. This high individual variation could partly explain the lack of significance, and a bigger sample size would be required to assess whether the lack of significance in the results emanated from a large individual variation. Similar to the two previous experiments in my thesis, bigger sample size and higher statistical power would help obtain stronger evidence and clearer interpretations of the results. However, Nicol and Pope (1996) used 12 hens in their experiment, and in mine 11 hens were used in the analysis (seven passed the training criteria and four were untrained). Therefore, given that previous studies have obtained strong evidence with relatively similar sample sizes to ours, the uncertainty of my results could be explained by other factors than sample size. However, both Nicol and Pope's (1996) and my study have large confidence intervals, suggesting that individual differences in the hens' behaviour have a big impact on the results.

In fact, when comparing hens in our experiment to those of Nicol and Pope's (1996) it can be seen that hens spent very different amounts of time pecking in the experiments. This could be one of the possible explanations for the difference in findings between this study and Nicol and Pope's (1996). Furthermore, the effect of training on the hens' foraging decisions is much weaker than in Nicol and Pope (1996). In fact, although hens trained on red ate more red food, they did not eat enough of it for the effect to be detected.

Moreover, in Nicol and Pope's (1996) experiment less than 1 peck in 1000 pecks was directed at the "opposite" food, both from the hens and the chicks. In this experiment, the response to "opposite" food was much more variable, both for hens and chicks, especially since chicks were not trained with a palatable and unpalatable food. Thus there was much more variation in how the hens and chicks behave, compared to Nicol and Pope's (1996). It is not known why there was much more variation in my experiment compared to Nicol and Pope's (1996), but this might explain why the results obtained are not similar to Nicol and Pope's (1996). In this experiment, food pecking, ground pecking and ground scratching did not seem to be influenced by the proportion of time chicks spent feeding on "opposite" food. Most of the results of this experiment may therefore stem from the fact that the hens might not have acquired a strong enough preference for one food, or that they did not acquire the knowledge that the other food was unpalatable.

Another potential limitation in this experiment is that both hens and chicks were food deprived before the conditioning period. However it is known that food deprivation of observers hinders social learning in hens (Nicol & Pope, 1993). Hens were food deprived so that they would increase their food pecking behaviour. Because hens and chicks were housed together in this experimental design, it was impossible to food deprive the hen without food depriving the chicks. This could further explain the lack of evidence of social learning of the chicks.

#### 7.5.2.2 Lack of replication

I failed to replicate Nicol and Pope's (1996) findings, which found that hens modify their behaviour when chicks feed from seemingly unpalatable food. There are many potential issues that can cause the lack of replication of a study such as differences between the original and replication studies that can affect the effect sizes, the original article being a false positive, or the replicated study being a false negative (Open Science Collaboration, 2015). Although care was taken to replicate Nicol and Pope's (1996) methods as closely as possible, there are several methodological difference that could account for the difference in observed results. First of all, despite increasing the quinine concentration, the hens in my study reacted very differently to the quinine than the hens in Nicol and Pope's (1996) study. In my opinion, the difference in reaction to quinine is the main factor behind the difference in result in the two studies. Secondly, because of the time restriction of my study, I used broody hens that were available, and the hens used in my study where from different breeds than those used in Nicol and Pope's (1996), this could have affect the individual variation observed in the study. However, both in Nicol and Pope's (1996) study and this study, three different breeds were used, in order to prevent breed specific result. Thirdly, unlike Nicol and Pope's (1996) study, the chicks in my study were not trained to learn that one food colour was unpalatable. This could also have influenced the hens' behaviour.

The lack of replication of Nicol and Pope's (1996) findings mirror a larger crisis within experimental psychology (Open Science Collaboration, 2015; Pashler & Wagenmakers, 2012). Replication is at the core of scientific process as it allows to increase certainty in the result produced in research. Researchers have however had difficulties in replicating well-known results in a variety of fields (Makel, Plucker, & Hegarty, 2012; Pashler & Wagenmakers, 2012). Although Makel et al. (2012) found that overall published replication studies report similar findings to those from the original studies, the Open Science Collaboration (2015) project, which replicated 100 studies published in psychology, found that only 39% of the effects were found to have replicated the

original results. In general, very few replication studies are published: Makel et al. (2012) report that only 1.07% of studies in psychology are replications, and the difference between Makel et al.'s (2012) and the Open Science Collaboration (2015) project could be due to a bias towards publishing replication studies that replicate the original result. Makel et al. (2012) further report that more than half of published replications are conducted by the same team as the one who produced the original article, and that alarmingly, replications from the same research team are more likely to be successful in reporting similar findings to the original study, than replications from a different team (Makel et al., 2012).

Publication bias, where there is a tendency to publish only positive findings, can also lead to an increased likelihood of false-positive findings being published (Forstmeier, Wagenmakers, & Parker, 2016). According to Forstmeier et al. (2016), the publication of false positives is expected to increase with a decreasing sample size, an increasing pursuit of novelty, various forms of multiple testing and incorrect *p*-values, especially during pseudoreplication. The sample size in Nicol and Pope (1996) was indeed fairly small, and slightly smaller than most studies done on social learning in fowl (Cloutier et al., 2002; Nicol & Pope, 1992, 1993, 1994, 1999; Sherwin et al., 2002; Wauters & Richard-Yris, 2002; Wauters et al., 2002). This might have increased the change of getting a false positive. However, while Nicol and Pope's (1996) results are novel, they are in line with other findings on social learning in domestic fowl and hens being sensitive to potential threats to their chicks (Cloutier et al., 2002; Edgar, Paul, & Nicol, 2013; Nicol & Pope, 1992, 1993, 1994, 1999; Sherwin et al., 2002; Wauters & Richard-Yris, 2002; Wauters et al., 2002).

The lack of replication observed in psychology also stems from a heavy reliance on p-value significance testing (Wetzels et al., 2011). In order to avoid overinterpretation of *p*-values, Wetzels et al. (2011) suggests reporting the effect sizes and confidence intervals alongside of the *p*-value, or using a Bayesian approach. Bayes factors and *p*-values almost always agree about which hypothesis is better supported by the data, however, they vary in the strength of this support (Wetzels et al., 2011). Particularly, 70% of the data sets with *p*-

values between .01 and .05 are associated with a Bayes factor that the evidence is only anecdotal (Wetzels et al., 2011). Both significant results reported by Nicol and Pope (1996), fall within that range ($p = 0.02$ for food pecking, and $p = 0.04$ for ground scratching/pecking), which might mean that by using a Bayesian approach instead of a frequentist one, the results might have been classified as anecdotal. Regarding the effect sizes, although Nicol and Pope (1996) do not report them, I calculated the confidence intervals of their results, and was able to compare them to the ones I obtained. This allowed me to conclude that because of the overlap in confidence intervals between the two studies, the results of my study were not inconsistent with Nicol and Pope's (1996). Moreover, it should be noted that a single failure to replicate findings should not be treated as evidence against the exitence of an effect (Collaboration, 2012; Simons, 2014). Hence more replications of this study should be carried out.

#### 7.5.2.3 Future work

On top of replicating the experiment, other behavioural measures could be taken to look at potential teaching in fowl. Food calls are closely associated with food preference in hens (Nicol & Pope, 1999; Wauters et al., 1999) and Wauters and Richard-Yris (2002) found that the chicks' responses were strongly affected by food calls. In this experiment food calls were not recorded, but they could have been of importance in shaping the chicks' behaviour. Hence, there could have been a difference in response between displays containing food calls, and those that did not, which this experiment does not account for. Food calls were not recorded because Nicol and Pope (1996) did not find an effect of the chicks' seeming foraging errors on the food call production. Thus the food calls of hens in this experiment were not analysed. The importance of food calls in the white-tailed ptarmigan display, and its potential to being teaching behaviour (Clarke, 2010) raises the question of the role of food calls in domestic fowl for teaching, and although Nicol and Pope (1996) did not find any evidence of the number of food calls being modified, other aspects of food calls, such as call intensity (louder, faster, longer), could be. Thus, future work should include food call emission to replicate Nicol and Pope's (1996) findings.

More analysis could also be done in the way the foraging choices are measured. In this experiment, the amount of time each behaviour occurred was measured. When food pecking at different colours was measured, the number of pecks and the rate of pecking were also analysed. However, Moffatt and Hogan (1992) showed that the speed at which the chicks approached the hens increased with the intensity of the maternal display. On top of the latency to approach, other measures that could be included are the first choice, the latency to make that first choice as well the number of visits to each food choice. Those measures were not taken because of time constraints. Moreover, because not all pecks lead to ingestions, the time spent pecking is not correlated to the quantity of food ingested by chicks (Hogan, 1971). However, video footage does not allow an experimenter to reliably determine what food items are ingested or not by the chicks. Hence, if the amount of pecking is not linked to the amount of ingestion, then the pecking behaviour of chicks might not be indicative of their preference, which could explain why little evidence of the hens' pecking behaviour on the chicks' was obtained.

#### 7.5.2.4 Maternal display in hens

The sight of chicks inhibits mother's feeding and prolongs the maternal display (Sherry, 1977). Moreover Stokes (1971) shows that the display of red junglefowl is more intense when the chicks are too far or fail to respond: hens were found to vocalise louder, faster and longer when their chicks were further from them. The display is also prolonged when both visual and vocal contact between the chick and its mother are lost (Sherry, 1977). Similar results were found in domestic chickens, where Wauters et al. (1999) showed that hens emit longer and more food calls when their chicks are visible but physically separated from the hens. Furthermore, in a non-foraging context, Edgar et al. (2013) found that hens adjusted their behavioural responses based on their knowledge when they perceived their chicks to be threatened, regardless of their chicks' distress. Given the amount of findings reporting that hens adjust their behaviour based on their chicks' behaviour and their own knowledge of the situation, it is quite surprising that similar findings were not found in my experiment.

Moreover, Kruijt (1964) report that Burmese red junglefowl mother hens are often attracted by food-running chicks, where the hen would take over the prey and process it into manageable size for the chicks. Wauters and Richard-Yris (2002) also found that hens elicit more foraging sequences containing a food call when their chicks are not feeding, compared to foraging sequences without a food call. This further shows that hens are attentive to the chicks' foraging behaviour. Given the attention hens give to chicks' foraging behaviour, it should not come as a surprise that hens are able to acquire foraging information from their chicks.

Wauters and Richard-Yris (2002) showed that mother hens pay attention to the level of activity of their chicks and adjust their behaviour accordingly. Something similar could be happening in my experiment where instead of hens attempting to redirect their chicks' attention from the unpalatable to the palatable food, hens acquire information about the palatability of the second food through the behaviour of their chicks, because hens might not have acquired the information that one food was unpalatable during the training. The chicks' behaviour might act as encouragement or reinforcement, since hens ate more, and ate more of their training colour, when chicks pecked more at that same colour.

Several experiments have shown that brooded chicks follow their mother's foraging preference (Collias, 1952; McBride et al., 1969; Stokes, 1971; Wauters et al., 2002; Wood-Gush, 1971). Moreover, hens are sensitive to the extent of demonstrators' preference for palatable food (Sherwin et al., 2002). Thus it was expected that chicks would also be sensitive to the extent of the demonstrator's preference. However, most of the experiments made in this context give access to the same food for hens and chicks simultaneously. Moffatt and Hogan (1992) also showed that with an increase in intensity of the display, the speed at which chicks approach the hen and attempt to peck at the food she demonstrated increases. However in my experiment, hens and chicks were separated by mesh wire during the conditioning period, so the chicks could not respond naturally or simultaneously to the hens' display. If local enhancement

rather than stimulus enhancement plays a crucial role in the chicks' acquisition of foraging preference, then this could be a reason why there was little evidence of a transmission of preference from the mothers to the chicks. The experimental design did not allow local enhancement to occur, which might be one of the reason why no reaction of the chicks to an increase of the mothers' display was observed. In Nicol and Pope's (1993) experiment, non-deprived birds seemed more attentive to the behaviour of the demonstrator. Gajdon et al. (2001) further showed that although chicks can learn by visual observation, they are less successful at acquiring social information when access to food is restricted during the demonstration. This further highlights the importance of local rather than stimulus enhancement in the chicks' learning of foraging preferences.

There are several potential reasons why the expected results were not obtained in our experiment, and why the chicks' foraging choices did not seem to be influenced by the extent of the demonstrators' preferences. However, the lack of social transmission of information from the mother to the chicks could simply have been a function of the inadequate maternal display as most hens pecked at both foods during conditioning.

# Chapter 8:

# General Discussion

In my thesis, I explored three potential cases of teaching behaviour in nonhuman animals, all set in a foraging context. In this chapter I summarise the principal findings of the thesis and investigate alternative functions for the observed behaviour. Finally, I consider future directions for those three cases, and for teaching in general, highlighting further questions that need to be considered when studying teaching in animals.

## 8.1 Summary of findings

### 8.1.1 Food transfers in golden lion tamarins

In Chapter 5, I investigated the role of food transfers in shaping the foraging choices of wild golden lion tamarin juveniles. Previous evidence from a study conducted in captivity had established that novel and prior-adult sampled foods were transferred from adults to juveniles more than familiar food, suggesting that adults might teach juveniles what foods to incorporate into their diet (Rapaport, 1999). Although I found a similar trend, there was no evidence that adults modified their food transfer patterns in a statistically meaningful sense. Some factors other than teaching, that might also have explained the observed pattern of food transfer behaviour, were ruled out as alternative explanations. For instance, the data showed that juveniles (potential pupils) did not attempt to obtain more novel food compared to familiar food. Moreover, once they were engaged in a transfer in which the adult showed resistance to transfer the food, juveniles did not seem more motivated to obtain novel food compared to familiar foods. In fact, juveniles were as successful in obtaining novel or familiar food when I analysed only the transfers in which adults resisted. Juveniles were however more likely to attempt a transfer if they had ingested that type of food previously. Furthermore, in principle, any pattern in transfer could be explained by adults' preference for the familiar food, which could lead them to discard the novel foods more readily. This however did not seem to be the case as adults resisted attempted transfers of novel foods as much as attempted transfers of familiar foods, implying an inclination to keep novel foods as much as familiar foods. Hence, juveniles are not responsible for the food

transfer pattern observed, and adults do not seem to discard novel foods more than familiar ones.

One novel finding that came from examining the food transfer patterns was that transfers were more successful when the donor had already had experience ingesting a particular type of food. This suggests that donors have to be knowledgeable about the food palatability before transferring it.

One additional novel insight from my study was that, when looking at the mechanisms underlying juveniles' foraging choices five months after their first encounter with the experimental set up, it appeared that food transfers, particularly successful food transfers after which juveniles ingested food, were a good (and positive) predictor of juveniles' foraging choices. Individual exploration was also a good (and positive) predictor of the juveniles' choices. This extends Rapaport's (1999) study, which did not consider the longer-term effects of food transfers on juveniles' behaviour, in showing that food transfers are a good predictor of future foraging choices made by juveniles once they are independent. It is possible that experience with a food, via a food transfer or otherwise, drives this pattern, however it is unlikely because eating was not found to be a good predictor of the juveniles' choices.

Given that there was little evidence that adults modify their behaviour to transfer preferentially novel food, but that juveniles learn from food transfers, it is highly likely that the primary function of the transfers is nutritional, and that the learning that occurs is a by-product.

### 8.1.2 Food-offering calls in golden lion tamarins

In Chapter 6, I examined whether the role of food-offering calls was to teach the juveniles which substrate to forage on. Usually, food-offering calls are used by adults prior to a food transfer to indicate the donor's willingness to transfer food to the recipient (Boinski et al., 1994; K. Brown & Mack, 1978; Ruiz-Miranda et al., 1999). There are also reports of 15 instances where a food-

offering call was not emitted prior to a food transfer, but instead was emitted when an adult had been foraging for food, but was not observed to retrieve any (Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002). In each of these instances, a juvenile approached, and on seeing no food in the adult's hand, started foraging where the adult had been doing so. Juveniles then foraged and retrieved a food item from under vegetation, and adults did not interfere with the juveniles' foraging (Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002). Rapaport initially proposed that as the juveniles grow older, adults start using food-offering calls to direct the juveniles' attention towards a particularly profitable substrate, which provides them with an opportunity to learn where to forage independently.

I used a playback experiment to test whether juveniles learned from food-offering calls. I predicted that if juveniles did learn from the calls, they would eat more on a novel substrate, particularly after they had become independent foragers. The findings of this experiment are consistent with the teaching hypothesis: I found that juveniles that had experienced the playbacks ate more from the novel substrate even five months after the playbacks had initially been broadcast, compared to juveniles that had not experienced the playbacks. This is evidence for the third criteria of Caro and Hauser's (1992) definition. Immediate effects of food-offering calls were also observed in relation to interaction and insertion behaviour, but those did not last in the long-term, suggesting that a behaviour has to be coupled with a reward (ingestion) for food-offering calls to have long lasting effects.

Juveniles were also found to become more efficient at extracting food from the novel substrate between the training and testing phase. This could be because in the testing phase, juveniles have had prior experience with the substrate, and are subsequently more efficient, or because they have gained extractive foraging skills outside of the experiment and are then using their skill in the context of the experiment. Either way, juveniles learned how to extract embedded food items through time. Thus it appears that both social and asocial learning combine to allow the development of foraging skills.

In Chapter 6, I also looked at the changes in juveniles' behaviour over time, across each trial. The analysis found that the differences between the control and experimental conditions diminished over time, particularly in the testing phase. This suggests that, if food-offering calls function to teach juveniles about an appropriate substrate in which to forage, they do not teach them something that they would not be able to acquire otherwise, but rather that they accelerate learning, teaching them something earlier in life than they would have learned otherwise.

### 8.1.3 Maternal foraging behaviour in domestic fowl

In Chapter 7, I adapted Nicol and Pope's (1996) procedure to look at the modification of a hen's maternal display when faced with her chicks feeding from seemingly unpalatable food, and extended it to investigate whether chicks would learn what food to feed from by observing their mother. Unlike Nicol and Pope (1996), I did not find that hens increased their food pecking, ground pecking and ground scratching behaviour when chicks increased the proportion of time spent eating on opposite food (opposite to the food colour that the hen was trained on) compared to similar food. This could be explained by the (lack of) strength of the effect of the hens' training. In my experiment the effect of training was weaker than in Nicol and Pope's (1996). However, those findings are not inconsistent with Nicol and Pope's (1996) as there is a large overlap in the 95% confidence intervals between my data and Nicol and Pope's (1996).

In Chapter 7, I also presented data showing a (weak) positive correlation between the hens' and the chicks' foraging choices during conditioning. When looking at this correlation in a finer analysis, I found that hens' foraging choice was affected by observing the chicks' foraging choice in the five-minute period prior to the hens' decisions. This was however not the case for chicks, who were very consistent with their initial choice regardless of the hens' behaviour. Moreover, the similarity between the feeding choices of the hens and the chicks was not affected by the maternal display. This could also be explained by the weak training of the hens prior to the experiment.

Regarding longer-term acquisition of knowledge, I found that chicks' choices in the preference tests were highly consistent with their choices during the conditioning period, even up to ten days afterwards. Hence, once chicks are familiar with a food type, they tend to retain that preference when selecting their diet. This somewhat contradicts previous findings that showed that chicks would peck at anything, even if it could kill them, and require social information to select their diet (Hogan, 1984).

## 8.2 Examination of the three criteria, and alternative explanations for the observed behaviour

### 8.2.1 First criterion

The first criterion of Caro and Hauser's (1992) relates to the modified behaviour of the tutor in the presence of a naïve observer. More data has yet to be collected on the first criterion of Caro and Hauser's (1992) in the two species studied in this thesis. Although novel food items have been found to be transferred more than familiar ones in a study in captive GLTs (Rapaport, 1999), this was not found to be the case in my study. It is therefore possible that food transfers have purely a nutritional purpose. In my experiment, the observed food transferred were only fruits, not insects. Transfer rates in the experiment were also quite low compared to previous findings (Rapaport, 1999; Tardif et al., 2002), which could be explained by the fact that fruit pieces are not the type of items that are usually transferred. Live insects are food items that are usually transferred in the wild (Rapaport, 2006; Ruiz-Miranda et al., 1999); and it would be interesting to repeat the experiment using disabled or frozen insects. However, ethical and practical considerations prevented me from doing so in my experiment. Using live insects would have meant keeping a colony at the field station and running the risk of them escaping either from the colony or from the foraging platforms before the GLTs got to them. This was a particularly big risk for the crickets. It also would not have been possible to incapacitate the insects to prevent them from escaping during the experimental trials, by freezing them prior to each trials, because, given the climate, there were high chances of them thawing before I would have had the time to encounter the GLTs. Instead I used

dehydrated (dead) insects, which are commonly eaten by captive callitrichids (G. R. Brown et al., 2005; Rapaport, 1998, 1999; Vitale & Queyras, 1997; Voelkl et al., 2006), but were very rarely touched by the GLTs in my experiment. Callitrichids also typically transfer difficult to process food (E. C. Price & Feistner, 1993), which could help juveniles learn manipulative skills. Hence, in future experiments it would be interesting to include these as foods available for transfer. Therefore, it is possible that although there was no evidence for teaching through transfers of novel food in this experiment, GLTs might still teach their young what foods are good to eat through transfers of insects rather than fruits, or might teach them how to correctly manipulate those prey, as observed in meerkats (Thornton & McAuliffe, 2006). More data therefore need to be collected on a wider range of food types as well as on a wider range of subject age in the wild, for the results to provide a conclusive test of teaching in the food-transfer context.

In the context of food-offering calls in wild GLTs, a wider age range should also be tested. This would allow a better understanding of whether the calls are used to teach juveniles on what type of substrate to find food once they start foraging independently but are not quite proficient at it yet, as suggested by Rapaport (Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002). For the food-offering calls, there are also only 15 reported cases of those calls being used in a potential teaching context, rather than in a context in which they signal an inclination to transfer food (Rapaport, 2011; Rapaport & Ruiz-Miranda, 2002). Further data need to be collected to examine how widespread food-offering calls are in a putative teaching context, or whether they are mainly used prior to food transfers. Investigating the first criterion in the food-offering call context could also be done experimentally. For instance, in some GLT groups, adults could be trained to learn that a novel substrate contained food, and this substrate would then be hidden. In other groups, all individuals (both adults and juveniles) would be made aware of this novel substrate. It would then be possible to test whether adults emit more food-offering calls directed at juveniles in the first condition compared to the second. However, it would prove very difficult to isolate particular individuals to give them individual knowledge.

Moreover, in this food-offering call experiment, although I found suggestive evidence that juveniles learn from the playbacks (third criterion) which fits with the teaching hypothesis, the results are also consistent with alternative explanations for the function of food-offering calls. For instance, food-offering calls could be used by adults to recruit juveniles to a good foraging location, rather than to teach them about the foraging patch. Although there is evidence of learning, this could have been a by-product, rather than the function of the call.

Data also need to be collected to further understand the extent of the use of modified foraging displays in domestic fowl given that my study failed to replicate Nicol and Pope's (1996) findings, but yet, were not inconsistent with them. It is possible that the hens in my experiment did not behave as expected because of their training. Moreover, the high variability of the hens' behaviour could have obscured the teaching process in my experiment, but not in Nicol and Pope's (1996) by chance, or there could be no underlying teaching process and Nicol and Pope (1996) got a chance result. This difference in findings also contributes to the growing lack of replication of studies in experimental psychology (Pashler & Wagenmakers, 2012). It would therefore be interesting to replicate the procedure, with hens trained to a higher standard, and perhaps investigate other aspects of the maternal foraging display, such as food calls.

### 8.2.2 Second criterion

The assessment of the cost of each putative teaching behaviour also needs to be evaluated further. Clear experimental data are still needed in all three cases to provide a more accurate assessment of Caro and Hauser's (1992) second criterion, and proxy measures could be used. For instance, several groups of GLTs are habituated to humans at the Poço das Antas research station, which could permit the use of similar methods that were used to assess the cost of putative teaching behaviour in pied babblers and meerkats (Raihani & Ridley, 2008; Thornton & McAuliffe, 2006). Specifically, scales could be installed at some of the feeding platforms, where the weight of individuals could be assessed prior

to and following the teaching experiments. This could allow a comparison between weight loss and number of teaching events, as in the pied babblers. Other measures of cost, such as the delay until the next foraging bout following a teaching bout (e.g. food transfer or food-offering call in a non-food-transfer context) versus a non-teaching bout, or opportunity loss, could also be used to assess the costs of teaching in GLTs. Energetic costs can also sometimes be measured directly (Bennett, 1986). However, because it requires measuring oxygen flow, this would be easier to do in captivity, for instance with the domestic fowl. With this species, using proxies such as weight gain or loss, or through opportunity would not measure the cost adequately given that they are usually fed *ad libitum* outside of the experiment. One way to get around this would be to experimentally manipulate the feeding rations that the hens receive, and examine whether hens that are fed more are more likely to exhibit their maternal foraging display, compared to hens that are fed less.

### 8.2.3 Third criterion

More detailed work is also required to investigate the learning that results from putative teaching behaviour, for both species included in this thesis. For instance, in the food-transfer experiment conducted with GLTs, instead of conducting analyses on the aggregated data (i.e. collated across each phase), the learning criterion can also be assessed using more refined, time-varying models. I have already undertaken work using more dynamic Bayesian models, in collaboration with Daniel van der Post and James Ounsley, where we used the *Softmax* function to predict juveniles' foraging choices. Here, we fitted the likelihood that a particular food type has been chosen, given that a focal individual has chosen to eat that food type. Compared to the models presented in Chapter 5 (5.3.7.2), these models do not assume a linear relationship between previous experience and foraging choice, and also allow feedback to occur between events to investigate how previous events update individuals' attraction to specific food choices. This allows a more realistic analysis of the potential underlying mechanisms at play in the juveniles' foraging decisions, similar to the MCMC model used by Hoppitt et al. (2012) to study social learning

mechanisms in meerkats. We compared five models: (1) a non-learning model (where the initial attraction for each food type is fixed and not updated after each event); (2) a learning without social influences model (where the associations to food types are updated only after *eating* events); (3) a model that included asocial learning as well as transient social influences on learning (where stimulus enhancement can take place through observing other individuals eating that food type or due to a food transfer); (4) a model that included asocial learning, transient as well as direct social influence on learning (where observation and food transfer directly lead to learning); and, (5) a model similar to (4) that also included satiation and depletion (temporary decrease in the attraction to a particular food type).

Comparing the five models, we found the greatest support for the model that included asocial learning as well as transient and direct effect of social influences on learning. Depletion and satiation appeared to have little effect on the choices made by juveniles using this modelling framework. These analyses are still in progress, and we are planning to extend the framework to include all individuals, not just juveniles, in the future. We also set out to test different hypotheses about the role of food transfers in this species, by investigating the role of individuals' sex and age on receiver and donor behaviour, using a series of GLMMs in a Bayesian framework. These models suggest that overall females receive more transfers than males, juveniles receive more transfers than subadults, and subadults receive more transfers than adults. Regarding the donors, there were no clear patterns, but some indication that subadult females were transferring food more than others. In the future, we plan to extend this Bayesian modelling framework to examine whether food transfer attempts are predicted by food familiarity or experience, thereby testing the robustness of the results presented in Chapter 5 using more refined analytical methods.

Regarding food-offering calls, there was suggestive evidence that juveniles learned to forage more efficiently from the novel substrate after experiencing the playbacks. However the case would be stronger if a control playback (such as another GLT vocalisation that was not a food-offering call, or a

sound from the environment) was used instead of no playback to rule out the possibility that any noise, rather than specifically food-offering calls, was responsible for the observed patterns. In this chapter, it was also found that playbacks only had an effect on juveniles, but not on adults (see 8.4.4 below, and Appendix 8.A). This suggests that as juveniles grow up they learn not to respond to the calls any more. If this is the case, it also suggests that juveniles learn to respond to those calls in the first place. Hence it would be interesting to examine how juveniles associate calls with food when they are very young, and if this constitutes a case of teaching similar to what was found in pied babblers (Raihani & Ridley, 2008).

In Chapter 7, there was a little evidence that chicks learned from observing hens. Because chicks have been shown to use social information in many other contexts (Moffatt & Hogan, 1992; Nicol, 1995, 2004, 2006; Sherry, 1977; Stokes, 1971; Wauters & Richard-Yris, 2002; Wauters et al., 2002), in my opinion, the most likely reason for this is the weakness of the hens' demonstration.

## 8.3 Broader considerations

### 8.3.1 Benefit of teaching

My findings in GLTs and domestic fowl were each limited by the small sample sizes. Therefore more data are required before conclusive and generalizable inferences can be drawn, especially given the individual-level variation in behaviour that was observed. I found that food transfers are an important factor predicting juveniles' foraging choices (Chapter 5) and that juveniles forage more from a novel substrate when it has been associated with food-offering calls (Chapter 6). Teaching in GLTs could therefore be a strategy to speed the learning of valuable skills and information, and thereby reduce the burden of provisioning by hastening the transition to independent foraging. However, in Chapter 5, there was no evidence that GLTs modified their behaviour in a way that was consistent with the first criterion of Caro and Hauser's (1992) definition, and in Chapter 6, I did not investigate this first

criterion, hence the results are also consistent with alternative explanations where learning is a by-product rather than the function of those behaviour. Likewise, in domestic fowl, previous findings (Bartashunas & Suboski, 1984; Gajdon et al., 2001; Johnston et al., 1998; McQuoid & Galef, 1992, 1993; Salva et al., 2009; Suboski, 1984; Suboski & Bartashunas, 1984; Tolman, 1967a; Turner, 1964; Wauters & Richard-Yris, 2002; Wauters et al., 2002) suggest that social information is important for chicks to acquire correct dietary preferences because they are unable to distinguish between palatable and unpalatable food items. Teaching in this species would therefore increase the probability that juveniles learn the correct choice by attracting their attention *towards* palatable and *away from* unpalatable food items. However, in my experiment I found little evidence supporting teaching in this species.

### 8.3.2 Individual variation in teaching behaviour and sex biased dispersal

Both in GLTs and domestic fowls, I found a lot of individual variation in (allo-)parental investment and putative teaching investment. Individual variation was also found in other species. For instance, Kleindorfer et al. (2014) found that females adjust their investment in teaching behaviour based on the predation risks. Raihani and Ridley (2007) also found that subordinates, who are younger and have less foraging skills than dominants, will decrease the efforts they put into teaching when there are fewer resources available. Thornton (2008) also found individual variation in contributions to teaching behaviour in meerkats, which varied with the costs experienced by the teachers. For instance, younger meerkat helpers invested less in teaching because they were still investing in their own growth. However, Thornton (2008) found no effect of sex of the helper on investment in teaching. On the other hand, pied babbler males have been found to invest more in teaching behaviour than females (Raihani & Ridley, 2008). This could be because males stay longer in their natal area, and therefore benefit more from that investment than do females. In fact, Nelson-Flower et al. (2012) found a female-biased sex dispersal in this species, but only when considering dominant individuals alone. This was however only examined through the distance of dispersal rather than the delay.

In GLTs, data suggest that there are no sex differences in the age of dispersal for individuals that disperse, however more males than females appear to disperse, despite the data showing a lot of individual-level variation (Baker et al., 2002). In wild GLTs, males are also more likely to successfully integrate into a new group compared to females, and immigration is typically male-biased. Females inherit their mothers' territory when the mother dies, but sons do not inherit their fathers' territory (Baker et al., 2002). This creates fewer opportunities and less need for females to emigrate from their natal group.

Sex-biased help could follow two patterns: either adults help the sex that stays longer in the group, as this sex will help raise the young (Clutton-Brock et al., 2002), or adults help the dispersing sex when resources are limited, to increase the reproductive opportunities of the offspring (Ridley & Huyvaert, 2007; Ridley & Raihani, 2007). Very few sex differences were found in my data. However, in the food-transfer experiment in GLTs (Chapter 5), when analysing food transfer success, I found that juvenile females received slightly less food than juvenile males in the first phase of the experiment (in the second phase, the new juveniles were all females, so this analysis could not be conducted). This would support the hypothesis that in GLTs, adults preferentially support the development of the dispersing sex. When analysing food-transfer patterns for juveniles that were new in the second phase, there was a strong effect of the sex of the helper, with female adults being engaged in more food transfers than male adults. This parallels findings of differential investment in teaching according to the sex of the helpers found in pied babblers. In pied babblers, helpers (but not parents) favour young of the opposite sex, potentially because it decreases competition for breeding opportunities (Ridley & Huyvaert, 2007). However, the effect of the sex of the helper was not found when examining the patterns of food transfer in the first phase. Hence this lack of effect in the first phase could either be an effect of the sample size, or there could be an interaction of sex with season and resource availability. In fact the first phase took place at the end of the summer/ beginning of fall, and the second phase at the end of winter/ beginning of spring when a lot more fruits were available (pers. obs). Such adjustments are consistent with the observations that superb fairy-wrens, pied babblers and

meerkats where found to adjust their investment based on the cost of teaching and ecological constraints (Kleindorfer, Evans, et al., 2014; Kleindorfer, Hoi, et al., 2014; Ridley & Raihani, 2007; Thornton, 2008).

### 8.3.3 Teaching mechanisms

Although not all of my experiments explicitly examined the mechanisms underlying the learning of the pupil, in all cases stimulus enhancement is probably the most plausible option (see Table 8.1 for definitions of the mechanisms mentioned here). In fact, in the food transfer experiment in GLTs, successful food transfer seemed to be important for the juveniles' food choice. This behaviour allows juveniles to associate the reward of a particular food type with a social situation. In the food-offering call experiment, the playbacks appeared to attract juveniles to the novel substrate, which led to an increase in interaction, insertion and eating behaviour on that substrate compared to juveniles that did not have playbacks. This is suggestive of stimulus enhancement. In the domestic fowl experiment, chicks never had access to the food the hen was eating, which rules out local enhancement but suggests stimulus enhancement could be operating, if there had been any evidence of social learning. Social facilitation could also have played a role since chicks were generally more active during conditioning when the mother was present, than during the preference tests, when she was not present. In the GLT experiments, it was not possible to test for social facilitation because all individuals of each group had access to the experiments simultaneously. However the general level of activity in those groups might have varied which could have influenced the juveniles' decisions.

Although I did not find evidence supporting the first criterion of Caro and Hauser's (1992) definition, in terms of the tutor's behaviour, in domestic fowl, previous research reported that the form of putative teaching most resembles coaching, since hens were found to potentially attract chicks away from unpalatable food (Hoppitt et al., 2008; Nicol & Pope, 1996). In contrast, for the GLTs, the tutor's behaviour most resembles opportunity providing, given

previous research. This is similar to teaching in meerkats (Thornton & McAuliffe, 2006), but instead of providing the opportunity to learn a skill, adult GLTs provide juveniles with the opportunity to learn what food type they should incorporate into their diet (in the food transfer experiment) or what substrate they should forage on (in the food-offering call experiment).

Table 8.1: Definitions of the social learning mechanisms from Hoppitt and Laland (2013)

| Mechanism | Definition | Source |
|---|---|---|
| Stimulus enhancement | Observation of a demonstrator (or its products) exposes the observer to a single stimulus at time $t_1$, and single stimulus exposure effects a change in the observer detected, in a behaviour, at $t_2$. | Heyes (1994) |
| Local enhancement | An observer is more likely to visit or interact with object at a location after having observed a demonstrator visit or interact with an object at that location. | Thorpe (1963) |
| Social facilitation | The presence of a demonstrator affects the observer's behaviour. | Zajonc (1965) |
| Coaching | When the response of a demonstrator to the behaviour of the observer acts to encourage or discourage that behaviour. | Caro and Hauser (1992) |
| Opportunity providing | When the products of the behaviour of the demonstrator provides the observer with an opportunity to engage in operant learning that would otherwise be unlikely to arise. | Caro and Hauser (1992) |

## 8.4 Future directions for the study of teaching behaviour

### 8.4.1 Investigating putative cases of teaching behaviour

Although some researchers are not interested in reporting whether a species teaches or not (e.g. Kline, 2015), applying a systematic definition to the study of teaching would allow for more effective comparisons between and within species of the different types of teaching that are observed (Caro, 2015; Caro & Hauser, 1992). Only then, after we have acquired detailed examples of teaching across a broad range of taxa, can we start to answer more refined questions about the conditions necessary for teaching to evolve. The role played by the socio-ecological environment is one important factor that requires further consideration, for instance. Whether the putative cases of teaching behaviour evolved for teaching purposes and function to facilitate learning, or whether

learning is a by-product of another behaviour (e.g. food sharing), is another question to consider. Moreover, the mechanisms that underpin teaching, and appear to vary between species, are also currently largely unknown, and require clarification. The collection of further data across different taxonomic groups, and across contexts in which teaching might occur, will shed light on all of these important questions. If a unique definition is adopted, such data could also shed light on the differences between human and animal teaching. In the anthropological and psychological literature, teaching is often confirmed based on less stringent criteria than is expected for non-humans. For instance, in humans, teaching is often assumed based either on the modification of behaviour of the tutor (first criterion) or by the intent of the tutor to teach, but without examination of whether the pupil learns as a result (e.g. Ronfard, Was, & Harris, 2016). To my knowledge, there is also very little investigation of the cost of teaching in humans. Both the cost to the tutor and the learning outcome of the pupil are crucial in Caro and Hauser's (1992) definition of teaching behaviour, therefore it is important that equivalent criteria are adopted when making informative comparisons between human and nonhuman teaching behaviours. In my opinion, a definition applicable across species focusing on the function of the behaviour, would then allow for comparisons between humans and non-humans to take place based on the different mechanism involved.

### 8.4.2 Human teaching, theory of mind and brain development

Teaching in humans has often been considered different from teaching in nonhuman animals, because of humans' use of language and potentially of theory of mind when teaching (Csibra & Gergely, 2006; Strauss et al., 2002; Thornton & Raihani, 2008). However, there is, to my knowledge, no experimental connection between theory of mind and teaching (defined in a functional sense), other than one study examining a positive relationship between these two traits in the development of Western children (Strauss et al., 2002). Indeed, studies on non-human animals suggest that teaching behaviour can be progressively modified in a way that supports learning without the tutor having any understanding of the state of the pupil's knowledge (e.g. Thornton & McAuliffe, 2006). To examine

whether teaching requires theory of mind or the attribution of mental states in humans, a possible experiment could be conducted that compares the teaching abilities (i.e. ability to modify behaviour in order to facilitate learning in another individual) of individuals lacking or having impaired mental state attribution, with individuals who have normal functioning mental state attribution. It would also be interesting to understand how teaching manifests in the brain, and what role the different brain areas play in relation to this behaviour. It would likely prove informative to compare and contrast patterns of brain activation in both the brain of the tutor and the pupil, and it would also be interesting to examine whether there are differences in neural activation in relation to the different strategies and mechanisms used and performed during teaching. In children, there are some correlations between the development of teaching and theory of mind (Strauss et al., 2002); however it would be information to know whether these measures also correlate with patterns of neural development, which could be assessed using fMRI.

### 8.4.3 Tutors' prior knowledge

Tutors might need time to acquire the knowledge that is required to engage in effective teaching. In my study with hens, mothers could be trained separately from the young, and could acquire knowledge prior to engaging in putative teaching behaviour. However, separating the training of the tutors and pupils was not possible in either of the GLT studies because individuals were trained and tested in a group setting. It was therefore not possible to control for the prior knowledge of the potential tutors. Prior knowledge of the tutor is particularly relevant to the food transfer experiment, because if adults are teaching young what food to incorporate in their diet, it is expected that adults must first sample the food in order to know whether it is palatable or not. Thornton and Raihani (2010) point out that there is still no evidence of adults sampling the food prior to transferring it to juveniles, since GLTs transfer both familiar and novel food to their young (Chapter 5; Rapaport, 1999). However, I found evidence that food transfers were more successful when the donor had ingested the food option at least once, suggesting that donors do sample the food

before transferring it. Future studies in the wild should incorporate prior-sampled food in their experiments whenever possible to test whether adults treat these food types differently than novel foods. In Chapter 5, I found little evidence that prior-adult sampled foods were transferred to a greater extent than both novel and familiar food, however the sample size was too small to generalise.

### 8.4.4 The role of social information relative to that of individual information

It is also important to study the relative role of socially acquired information (such as that acquired through teaching) compared to individually obtained information. This is what I attempted to examine in the food-transfer experiment in GLTs (Chapter 5) by comparing the importance of asocial learning parameters such as exploration or eating, to the importance of social learning parameters, such as observation, scrounging and food transfers.

In the food-offering call in GLTs and maternal display in domestic hens experiments, investigating the relative role of social information and individual information could be done by giving individuals prior knowledge about a food type or substrate when on their own, and then providing them with another food type or substrate in a social context. In the food-offering call experiment with wild GLTs (Chapter 6), this could however be difficult to achieve as GLTs often move in groups, and it would likely prove difficult to attract only one individual to a novel substrate, without attracting the rest of the group. This would be particularly difficult if those individuals were juveniles given that they are heavily reliant on adults (Hoage, 1982; Ruiz-Miranda et al., 1999) and are always within close distance of them (pers. obs). In the domestic fowl experiment (Chapter 7), chicks were actually given prior information about a food type, and then given a choice of two food patches from which to forage: one about which they had prior information, and another from which they were given social information by the hen (in some of the conditions). It appears from my results that chicks were fairly conservative, but it would be interesting to know to what

extent chicks would rely on social information if they were not given prior information about one of the food types, or given stronger prior information by making one of the food types unpalatable to them.

The results from the domestic fowl experiment somewhat contradict previous research that showed that younger chicks are more likely to use social information compared to adults. My results instead suggest that chicks are conservative with their own knowledge, and that hens are more likely to use social information than chicks. It is however surprising that hens would copy chicks but not vice-versa. Regarding the use of social information and age, in the food-transfer experiment with GLTs, it has been shown that juveniles are not the only ones receiving food from others, but whether or not adults also learn from receiving food from transfers is still under investigation. In the food-offering playback experiment, further analysis not shown in Chapter 6 (see Appendix 8.A) revealed that there were no differences in eating behaviour in adults in the experimental and control conditions (both in the training and testing phase). Hence adults do not learn from playbacks of food-offering calls. Given that the calls are heard by all (or most) individuals in the group, this either suggests that juveniles are the targeted audience for these calls, or that only juveniles respond to them, as suggested by previous observational reports (Boinski et al., 1994; K. Brown & Mack, 1978; Ruiz-Miranda et al., 1999).

Another avenue of further research would be to investigate individual variation in the tutor and the pupil's behaviour, or in the pupil's preference for individual over social information. From observation, it appeared that the chicks, which were tested in pairs, often behaved differently from each other. There commonly appeared to be one chick in each pair that would consistently instigate movement or feeding behaviour, while the other would often follow. By comparing the chicks' inter-individual variation on their activity levels and leadership, it would be possible to investigate whether individuals that are more active and initiate movement always prefer to use personal information that they acquired previously (which could be why they are initiating movement), or if they are more likely to be flexible in their use of information, and base their

decision on a mix of personal and social information. As Beck (2015) points out, it would also be interesting to know if the experience of an individual as a learner has any impact on its behaviour as a teacher, and whether some individuals are better teachers than others. Differences in teaching could also be examined at a higher level, such as at the level of populations. This would be quite difficult in GLTs, given the small population size, and the fact that very few groups are habituated for such experiments. In domestic fowl this could however be more easily investigated by examining differences across and within breeds.

## 8.5 Conclusion

This thesis set out to investigate three cases of putative teaching behaviour. I added to this body of knowledge by investigating the cases of food transfers and food-offering calls in wild golden lion tamarins, and maternal display in domestic fowl. In Chapter 5, I found that adults did not transfer more novel food compared to familiar food to the juveniles (lack of evidence for the first criterion). However, transfers were more likely to be successful if the donor had previously ingested the food type involved in the transfer. I also discovered that previous successful food transfers seemed to be an important factor in predicting future foraging choices of juveniles (third criterion). In Chapter 6, I found evidence that juveniles learned from food-offering calls to forage from a novel substrate (third criterion). In Chapter 7, I was not able to replicate Nicol and Pope's (1996) findings that mother hens modify their behaviour in the presence of their chicks feeding from seemingly unpalatable food (lack of evidence for the first criterion), yet, my results were not statistically inconsistent with theirs. I also detected very little evidence that chicks learn from their mothers (lack of evidence for the third criterion); to the contrary chicks feeding preference appeared consistent with their own prior knowledge, which lasts for at least ten days after initial exposure. Moreover, instead of finding evidence that chicks use social information from their mothers, there was evidence that the hens used information about foraging patches from their chicks. Overall, further data and experiments are required in relation to each of these three putative cases of teaching behaviour in order unequivocally to classify them as teaching.

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# Appendix:

## Appendix Chapter 2:

**Appendix 2.A:** Ethical approval for the golden lion tamarin experiments

University of St Andrews

School of Biology Ethics Committee

27th March 2014

| | |
|---|---|
| **Project Title:** | **Investigation of teaching behaviour in Golden Lion Tamarins** |
| **Researchers Name(s):** | **Prof Kevin Laland, Carlos Miranda, Camille Troisi** |
| **Supervisor(s):** | **Prof Kevin Laland** |

Thank you for submitting your application which was considered by the Biology School Ethics Committee on the 27th March. The following documents were reviewed:

1. Animal Ethics Form 17/02/2014

The School of Biology Ethics Committee approves this study from an ethical point of view.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the condition that local permits are obtained prior to the project starting, and also on the understanding that the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (published in Animal Behaviour, 2003, 65, 249-255, http://www.sciencedirect.com/) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462157
The University of St Andrews is a charity registered in Scotland: No SC013532

Figure 2.A.1: Ethical approval from the University of St Andrews

Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

# Autorização para atividades com finalidade científica

| Número: 17409-9 | Data da Emissão: 09/08/2013 14:15 | Data para Revalidação*: 08/09/2014 |
|---|---|---|

* De acordo com o art. 33 da IN 154/2009, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

## Dados do titular

| | |
|---|---|
| Nome: CARLOS RAMON RUIZ MIRANDA | CPF: 053.754.227-27 |
| Título do Projeto: Manejo de metapopulação do mico leão dourado: pesquisa e ações | |
| Nome da Instituição : associação mico-leão-dourado | CNPJ: 39.509.559/0001-87 |



## Cronograma de atividades

| # | Descrição da atividade | Início (mês/ano) | Fim (mês/ano) |
|---|---|---|---|
| 1 | Monitorar grupos selecionados | 07/2010 | 08/2015 |
| 2 | Levantamento de ocorrencia de micos | 07/2010 | 08/2015 |
| 3 | Modelagem metapopulação | 07/2010 | 08/2015 |
| 4 | Manejo para conectividade entre populações | 07/2010 | 08/2015 |

## Observações e ressalvas

| | |
|---|---|
| 1 | As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia. |
| 2 | Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso. |
| 3 | Este documento somente poderá ser utilizado para os fins previstos na Instrução Normativa IBAMA n° 154/2007 ou na Instrução Normativa ICMBio n° 10/2010, no que especifica esta Autorização, não podendo ser utilizado para fins comerciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades científicas ou didáticas no âmbito do ensino superior. |
| 4 | A autorização para envio ao exterior de material biológico não consignado deverá ser requerida por meio do endereço eletrônico www.ibama.gov.br (Serviços on-line - Licença para importação ou exportação de flora e fauna - CITES e não CITES). |
| 5 | O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ. |
| 6 | O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio e o material biológico coletado apreendido nos termos da legislação brasileira em vigor. |
| 7 | Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen. |
| 8 | Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade. |
| 9 | As atividades contempladas nesta autorização abrangem espécies brasileiras constante de listas oficiais (de abrangência nacional, estadual ou municipal) de espécies ameaçadas de extinção, sobreexplotadas ou ameaçadas de sobreexplotação. |

## Outras ressalvas

| | |
|---|---|
| 1 | O pesquisador estrangeiro Carlos Ramón Ruiz-Miranda possui vínculo empregatício efetivo com a Universidade Estadual do Norte Fluminense Darcy Ribeiro. Dispensado de autorização do Ministério da Ciência e Tecnologia. |

## Equipe

| # | Nome | Função | CPF | Doc. Identidade | Nacionalidade |
|---|---|---|---|---|---|
| 1 | MARCIO MARCELO DE MORAIS JUNIOR | Pesquisador | 262.075.928-59 | 254412816 SSP/SP-SP | Brasileira |
| 2 | ADRIANA DAUDT GRATIVOL | Pesquisadora | 000.917.777-98 | 081741209 IFP-RJ | Brasileira |
| 3 | Andreia Martins | Pesquisadora | 927.144.207-53 | - | Brasileira |
| 4 | Synval de Melo | Monitor Micos | 418.931.407-25 | 1.360.708 - | Brasileira |
| 5 | Nelson Barbosa dos Santos | Monitor Micos | 002.703.257-43 | 068059302 IFP-RJ | Brasileira |
| 6 | Oberlan Cezar Cabral Junior | Monitor Micos | 096.989.297-70 | 12098439-8 DETRAN-RJ | Brasileira |



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**Código de autenticação: 49627963**

Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

# Autorização para atividades com finalidade científica

| Número: 17409-9 | Data da Emissão: 09/08/2013 14:15 | Data para Revalidação*: 08/09/2014 |
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## Dados do titular

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| Nome: CARLOS RAMON RUIZ MIRANDA | CPF: 053.754.227-27 |
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| Nome da Instituição : associação mico-leão-dourado | CNPJ: 39.509.559/0001-87 |



## Cronograma de atividades

| # | Descrição da atividade | Início (mês/ano) | Fim (mês/ano) |
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## Observações e ressalvas

| | |
|---|---|
| 1 | As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia. |
| 2 | Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso. |
| 3 | Este documento somente poderá ser utilizado para os fins previstos na Instrução Normativa IBAMA n° 154/2007 ou na Instrução Normativa ICMBio n° 10/2010, no que especifica esta Autorização, não podendo ser utilizado para fins comerciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades científicas ou didáticas no âmbito do ensino superior. |
| 4 | A autorização para envio ao exterior de material biológico não consignado deverá ser requerida por meio do endereço eletrônico www.ibama.gov.br (Serviços on-line - Licença para importação ou exportação de flora e fauna - CITES e não CITES). |
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| 7 | Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen. |
| 8 | Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade. |
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## Outras ressalvas

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Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
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## Autorização para atividades com finalidade científica

| Número: 17409-9 | Data da Emissão: 09/08/2013 14:15 | Data para Revalidação*: 08/09/2014 |
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| Nome: CARLOS RAMON RUIZ MIRANDA | CPF: 053.754.227-27 |
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| Nome da Instituição : associação mico-leão-dourado | CNPJ: 39.509.559/0001-87 |



Cronograma de atividades

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| 3 | Modelagem metapopulação | 07/2010 | 08/2015 |
| 4 | Manejo para conectividade entre populações | 07/2010 | 08/2015 |

Observações e ressalvas

| | |
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| 7 | Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen. |
| 8 | Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade. |
| 9 | As atividades contempladas nesta autorização abrangem espécies brasileiras constante de listas oficiais (de abrangência nacional, estadual ou municipal) de espécies ameaçadas de extinção, sobreexplotadas ou ameaçadas de sobreexplotação. |

Outras ressalvas

| | |
|---|---|
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Equipe

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| 3 | Andreia Martins | Pesquisadora | 927.144.207-53 | - | Brasileira |
| 4 | Synval de Melo | Monitor Micos | 418.931.407-25 | 1.360.708 - | Brasileira |
| 5 | Nelson Barbosa dos Santos | Monitor Micos | 002.703.257-43 | 068059302 IFP-RJ | Brasileira |
| 6 | Oberlan Cezar Cabral Junior | Monitor Micos | 096.989.297-70 | 12098439-8 DETRAN-RJ | Brasileira |

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**Código de autenticação: 49627963**

Figure 2.A.2: Permit from the ICMBio from 9/08/2013 to 8/09/2014

Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

# Autorização para atividades com finalidade científica

| Número: 17409-12 | Data da Emissão: 10/09/2014 12:17 | Data para Revalidação*: 10/10/2015 |
|---|---|---|

* De acordo com o art. 33 da IN 154/2009, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

## Dados do titular

| Nome: CARLOS RAMON RUIZ MIRANDA | CPF: 053.754.227-27 |
|---|---|
| Título do Projeto: Manejo de metapopulação do mico leão dourado: pesquisa e ações | |
| Nome da Instituição : associação mico-leão-dourado | CNPJ: 39.509.559/0001-87 |



## Cronograma de atividades

| # | Descrição da atividade | Início (mês/ano) | Fim (mês/ano) |
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| 1 | Monitorar grupos selecionados | 07/2010 | 08/2015 |
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## Observações e ressalvas

| | |
|---|---|
| 1 | As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia. |
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## Outras ressalvas

| | |
|---|---|
| 1 | Os pesquisadores estrangeiros CARLOS RAMON RUIZ MIRANDA e Malinda Dawn Henry estão vinculados, respectivamente, a programa de bolsa ou auxílio a pesquisa patrocinado pelo CNPq e pela CAPES. O membro da equipe estrangeiro Camille Aurelie Troisi está vinculado a programa de intercâmbio científico (Ciências Sem Fronteiras - University of St. Andrews). Dispensados de autorização do Ministério da Ciência, Tecnologia e Inovação. |

## Equipe

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|---|---|---|---|---|---|
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| 2 | ADRIANA DAUDT GRATIVOL | Pesquisadora | 000.917.777-98 | 081741209 IFP-RJ | Brasileira |
| 3 | Andreia Martins | Pesquisadora | 927.144.207-53 | - | Brasileira |
| 4 | Synval de Melo | Monitor Micos | 418.931.407-25 | 1.360.708 - | Brasileira |

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## Dados do titular

| Nome: CARLOS RAMON RUIZ MIRANDA | CPF: 053.754.227-27 |
|---|---|
| Título do Projeto: Manejo de metapopulação do mico leão dourado: pesquisa e ações | |
| Nome da Instituição : associação mico-leão-dourado | CNPJ: 39.509.559/0001-87 |



## Cronograma de atividades

| # | Descrição da atividade | Início (mês/ano) | Fim (mês/ano) |
|---|---|---|---|
| 1 | Monitorar grupos selecionados | 07/2010 | 08/2015 |
| 2 | Levantamento de ocorrencia de micos | 07/2010 | 08/2015 |
| 3 | Modelagem metapopulação | 07/2010 | 08/2015 |
| 4 | Manejo para conectividade entre populações | 07/2010 | 08/2015 |

## Observações e ressalvas

| | |
|---|---|
| 1 | As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia. |
| 2 | Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso. |
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Figure 2.A.3: Permit from the ICMBio from 10/09/2014 to 10/10/2015

**Appendix Chapter 5:**

**Appendix 5.A:** Tables of valid trials used in the food transfer experiment (Chapter 5: 5.3.4.1 and 5.3.4.2)

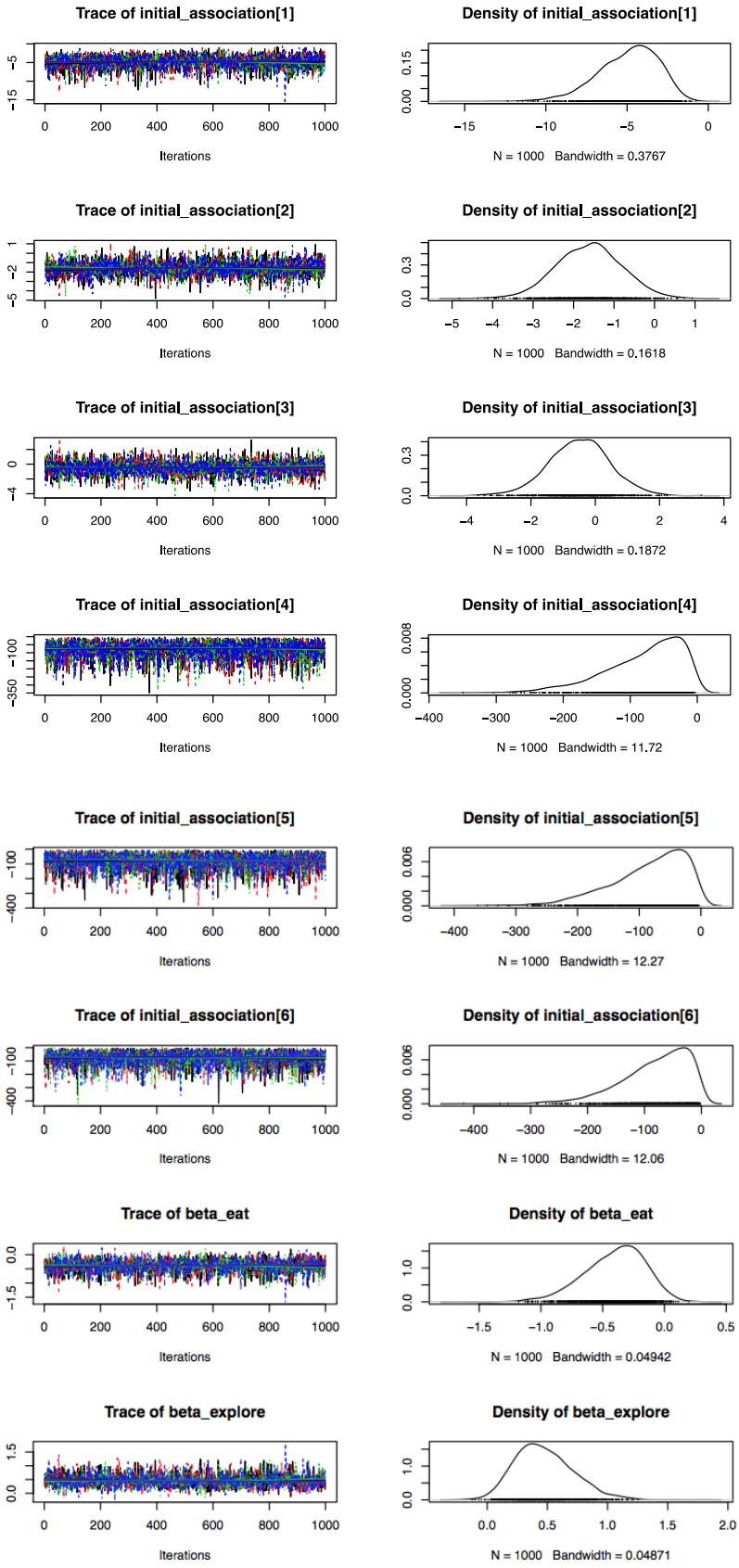
Table 5.A.1: Valid trials for the first phase

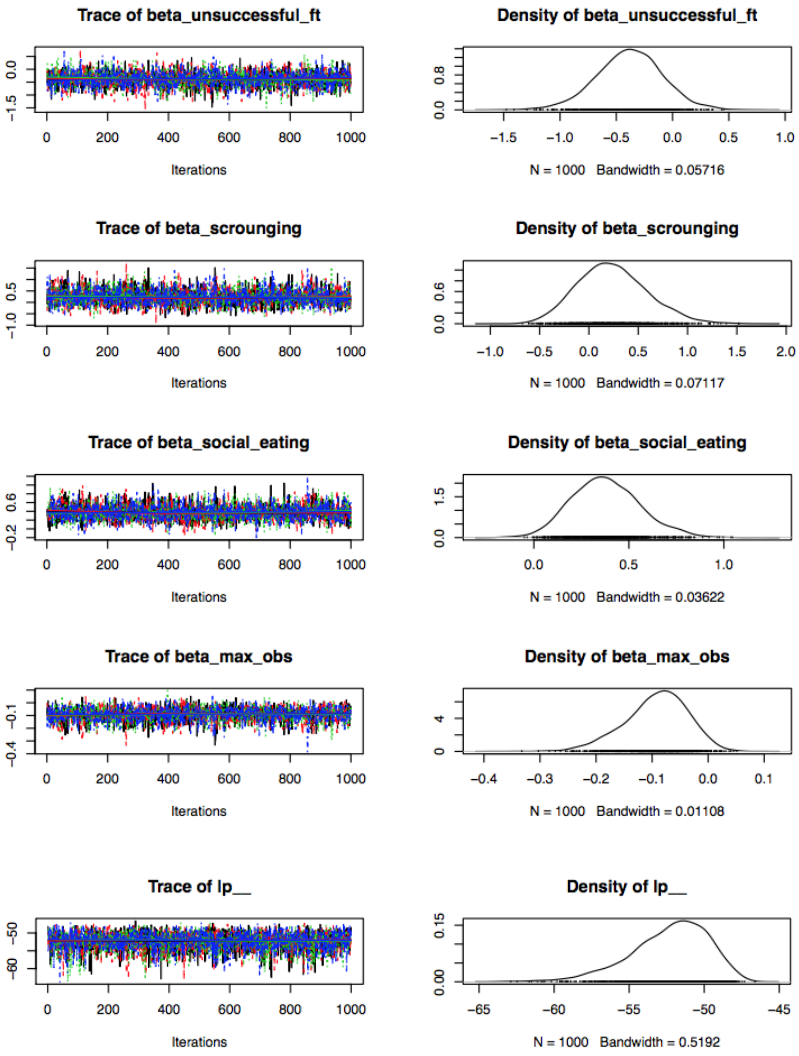
| Group | Trial 1 | Trial 2 | Trial 3 | Trial 4 | Trial 5 | Trial 6 | Trial 7 |
|---|---|---|---|---|---|---|---|
| BO2 | Valid | Valid | Valid | X | Valid | X | Valid |
| AF | Valid | Valid | Valid | Valid | Valid | ------ | ------ |
| Alone | Valid | Valid | X | Valid | Valid | Valid | ------ |
| AF2 | Valid | X | Valid | Valid | Valid | Valid | X |
| AF3 | Valid | Valid | X | Valid | Valid | Valid | ------ |
| Super | Valid | Valid | Valid | Valid | Valid | ------ | ------ |

Table 5.A.2: Valid trials for the second phase (AF2 was not included in the analysis)

| Group | Trial 1 | Trial 2 | Trial 3 | Trial 4 | Trial 5 | Trial 6 | Trial 7 | Trial 8 |
|---|---|---|---|---|---|---|---|---|
| BO2 | Valid | Valid | Valid | Valid | Valid | ------ | ------ | ------ |
| AF | Valid | Valid | Valid | Valid | Valid | ------ | ------ | ------ |
| Alone | X | Valid | Valid | Valid | Valid | X | Valid | ------ |
| AF2 | Valid | Valid | Valid | Valid | Valid | ------ | ------ | ------ |
| AF3 | Valid | Valid | Valid | Valid | X | X | Valid | Valid |
| Super | Valid | Valid | X | Valid | Valid | Valid | ------ | ------ |

**Appendix 5.B**: Traces and posterior distributions of all the parameters for the full model (Chapter 5: 5.4.2.2, Table 5.37). There is an *initial association* parameter for each food type, except for banana which is set to 0: 1: Apple, 2: Cricket, 3: Grape, 4: Mealworm, 5: Papaya, 6: Pear. "social eating" correspond to *successful food transfer*


Trace of initial_association[1]
Density of initial_association[1]
N = 1000 Bandwidth = 0.3767
Trace of initial_association[2]
Density of initial_association[2]
N = 1000 Bandwidth = 0.1618
Trace of initial_association[3]
Density of initial_association[3]
N = 1000 Bandwidth = 0.1872
Trace of initial_association[4]
Density of initial_association[4]
N = 1000 Bandwidth = 11.72
Trace of initial_association[5]
Density of initial_association[5]
N = 1000 Bandwidth = 12.27
Trace of initial_association[6]
Density of initial_association[6]
N = 1000 Bandwidth = 12.06
Trace of beta_eat
Density of beta_eat
N = 1000 Bandwidth = 0.04942
Trace of beta_explore
Density of beta_explore
N = 1000 Bandwidth = 0.04871
Iterations




**Appendix 5.C**: Parameter values and statistics for the models in the backward and forward stepwise model selection (Chapter 5: 5.4.2.3)

Table 5.C.1: A) First step of the backward stepwise model selection

| Parameters/ Stats | Model Fit Results (all Betas) | Model Fit Results (Without Eat) | Model Fit Results (Without Explore) | Model Fit Results (Without UFT) | Model Fit Results (Without Scrounging) | Model Fit Results (Without SFT) | Model Fit Results (Without Observation) |
|---|---|---|---|---|---|---|---|
| WAIC | 117.93 | 114.63 | 115.86 | 115.12 | 114.12 | 116.82 | 114.29 |
| LP | -58.19 | -53.19 | -53.87 | -52.51 | -51.87 | -53.81 | -52.86 |
| P_WAIC | 13.41 | 9.94 | 9.83 | 11.00 | 11.31 | 10.59 | 10.07 |
| PARS | 12 | 11 | 11 | 11 | 11 | 11 | 11 |

Table 5.C.1: B) Second step of the backward stepwise model selection (in the first step the best fitting model was the one without the *scrounging* parameter)

| Parameters/ Stats | Model Fit Results (Without Scrounging & Eat) | Model Fit Results (Without Scrounging & Explore) | Model Fit Results (Without Scrounging & UFT) | Model Fit Results (Without Scrounging & SFT) | Model Fit Results (Without Scrounging & Observation) |
|---|---|---|---|---|---|
| WAIC | 112.70 | 114.34 | 112.72 | 114.47 | 112.09 |
| LP | -52.66 | -53.41 | -52.41 | -53.25 | -52.76 |
| P_WAIC | 9.13 | 9.35 | 9.33 | 9.59 | 8.56 |
| PARS | 10 | 10 | 10 | 10 | 10 |

Table 5.C.1: C) Third step of the backward stepwise model selection (in the second step the best fitting model was the one without the *scrounging* and *observation* parameters)

| Parameters/ Stats | Model Fit Results (Without Scrounging, Observation & Eat) | Model Fit Results (Without Scrounging, Observation & Explore) | Model Fit Results (Without Scrounging, Observation & UFT) | Model Fit Results (Without Scrounging, Observation & SFT) |
|---|---|---|---|---|
| WAIC | 109.70 | 110.36 | 112.95 | 110.60 |
| LP | -52.67 | -52.94 | -54.16 | -52.87 |
| P_WAIC | 6.79 | 6.79 | 6.91 | 7.01 |
| PARS | 9 | 9 | 9 | 9 |

Table 5.C.1: D) Fourth step of the backward stepwise model selection (in the third step the best fitting model was the one without the *scrounging observation* and *eat* parameters)

| Parameters/ Stats | Model Fit Results (Without Scrounging, Observation, Eat & Explore) | Model Fit Results (Without Scrounging, Observation, Eat & UFT) | Model Fit Results (Without Scrounging, Observation, Eat & SFT) |
|---|---|---|---|
| WAIC | 110.03 | 110.14 | 109.51 |
| LP | -53.39 | -53.62 | -53.06 |
| P_WAIC | 5.84 | 5.48 | 6.02 |
| PARS | 8 | 8 | 8 |

Table 5.C.1: E) Fifth step of the backward stepwise model selection (in the fourth step the best fitting model was the one without the *scrounging*, *observation*, *eat* and *successful food transfer* parameters)

| Parameters/ Stats | Model Fit Results (Without Scrounging, Observation, Eat, SFT & Explore) | Model Fit Results (Scrounging, Observation, Eat, SFT & UFT) |
|---|---|---|
| WAIC | 109.54 | 109.95 |
| LP | -53.66 | -54.10 |
| P_WAIC | 4.96 | 4.49 |
| PARS | 7 | 7 |

Table 5.C.2: A) First step of the forward stepwise model selection

| Parameters/ Stats | Model Fit Results (without any Betas) | Model Fit Results (With Eat) | Model Fit Results (With Explore) | Model Fit Results (With UFT) | Model Fit Results (With Scrounging) | Model Fit Results (With SFT) | Model Fit Results (With Observation) |
|---|---|---|---|---|---|---|---|
| WAIC | 111.02 | 110.14 | 109.95 | 109.54 | 113.24 | 111.54 | 113.08 |
| LP | -55.24 | -54.18 | -54.10 | -53.66 | -55.81 | -54.86 | -55.66 |
| P_WAIC | 3.33 | 4.48 | 4.49 | 4.95 | 4.39 | 4.50 | 4.42 |
| PARS | 6 | 7 | 7 | 7 | 7 | 7 | 7 |

Table 5.C.2: B) Second step of the forward stepwise model selection (in the first step the best fitting model was the one with the *unsuccessful food transfer* parameter)

| Parameters/ Stats | Model Fit Results (With UFT & Eat) | Model Fit Results (With UFT & Explore) | Model Fit Results (With UFT & Scrounging) | Model Fit Results (With UFT & SFT) | Model Fit Results (With UFT & Observation) |
|---|---|---|---|---|---|
| WAIC | 110.04 | 109.56 | 112.22 | 110.25 | 111.04 |
| LP | -53.32 | -53.02 | -54.03 | -53.49 | -53.57 |
| P_WAIC | 5.96 | 6.04 | 6.59 | 5.94 | 6.36 |
| PARS | 8 | 8 | 8 | 8 | 8 |

Table 5.C.2: C) Third step of the forward stepwise model selection (in the second step the best fitting model was the one with the *unsuccessful food transfer* and *explore* parameters)

| Parameters/ Stats | Model Fit Results (With UFT, Explore & Eat) | Model Fit Results (With UFT, Explore & Scrounging) | Model Fit Results (With UFT, Explore & SFT) | Model Fit Results (With UFT, Explore & Observation) |
|---|---|---|---|---|
| WAIC | 110.84 | 112.70 | 109.87 | 113.66 |
| LP | -52.92 | -53.51 | -52.70 | -53.61 |
| P_WAIC | 7.15 | 7.82 | 6.92 | 8.50 |
| PARS | 9 | 9 | 9 | 9 |

Table 5.C.2: D) Fourth step of the forward stepwise model selection (in the third step the best fitting model was the one with the *unsuccessful food transfer, explore* and *successful food transfer* parameters)

| Parameters/ Stats | Model Fit Results (With UFT, Explore, SFT & Eat) | Model Fit Results (With UFT, Explore, SFT & Scrounging) | Model Fit Results (With UFT, Explore, SFT & Observation) |
|---|---|---|---|
| WAIC | 112.12 | 112.93 | 112.73 |
| LP | -52.83 | -53.09 | -52.64 |
| P_WAIC | 8.59 | 8.66 | 9.15 |
| PARS | 10 | 10 | 10 |

**Appendix Chapter 6:**

**Appendix 6.A:** Tables of valid trials used in the food transfer experiment (Chapter 6: 6.3.4.1 and 6.3.4.2)

Table 6.A.1: Valid trials for the training phase (AF2 was not included in the analysis)

| Group | Category | Trial 1 | Trial 2 | Trial 3 | Trial 4 | Trial 5 | Trial 6 | Trial 7 | Trial 8 |
|---|---|---|---|---|---|---|---|---|---|
| BO2 | Control | Valid | Valid | Valid | Valid | Valid | ------ | ------ | ------ |
| AF | Control | Valid | Valid | Valid | Valid | Valid | ------ | ------ | ------ |
| Alone | Experimental | Valid | Valid | X | Valid | X | Valid | Valid | ------ |
| AF3 | Experimental | Valid | Valid | Valid | Valid | Valid | ------ | ------ | ------ |
| Super | Experimental | X | X | Valid | Valid | Valid | X | Valid | Valid |

Table 6.A.2: Valid trials for the testing phase (AF2 was not included in the analysis)

| Group | Category | Trial 1 | Trial 2 | Trial 3 | Trial 4 | Trial 5 | Trial 6 |
|---|---|---|---|---|---|---|---|
| BO2 | Control | Valid | Valid | Valid | Valid | Valid | ------ |
| AF | Control | Valid | Valid | Valid | Valid | X | Valid |
| Alone | Experimental | Valid | Valid | Valid | Valid | Valid | ------ |
| AF3 | Experimental | Valid | Valid | Valid | Valid | Valid | ------ |
| Super | Experimental | Valid | Valid | Valid | Valid | Valid | ------ |

**Appendix Chapter 7:**

**Appendix 7.A:** Analysis of chicks' pecking behaviour during conditioning based on Nicol and Pope's (1996) behaviour

There was no evidence that the *similarity* between the chicks' and hens' food choices was influenced by the *total time spent by the hens ground pecking plus ground scratching* ($t = -1.80$, d.f. = 9, $p = 0.105$; see Fig. 6.A.1.B and Table 6.A.1) and by *the total time spent by the hens food pecking* ($t = 1.26$, d.f. = 9, $p = 0.239$; see Fig. 7.A.1.A and Table 7.A.1). The more the hens spent food pecking, the more the chicks and hens' food choices were similar, but the more the hen ground pecks and scratching the less similar the hens and chicks' choices are.

Table 7.A.1: Summary of the linear mixed model fitting the *similarity* between the chicks' and hens' choices given hen's *food pecking*, *ground pecking and scratching* behaviour

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | 1.55 | 0.85 | -0.12, 3.22 | 22 | 1.83 | 0.080 |
| Food Pecking | 0.004 | 0.003 | -0.002, 0.01 | 9 | 1.26 | 0.239 |
| Ground Pecking and Ground Scratching | -0.005 | 0.003 | -0.01, 0.001 | 9 | -1.80 | 0.105 |

Similar effects were found for the *similarity between the proportion of pecks* (*food pecking* (t = 1.12; p = 0.292); *ground pecking plus scratching* (t = -1.72; p = 0.120)) and for the *similarity in pecking rate* (*food pecking* (t = 0.65; p = 0.535); *ground pecking and scratching* (t = -0.08; p = 0.941)).

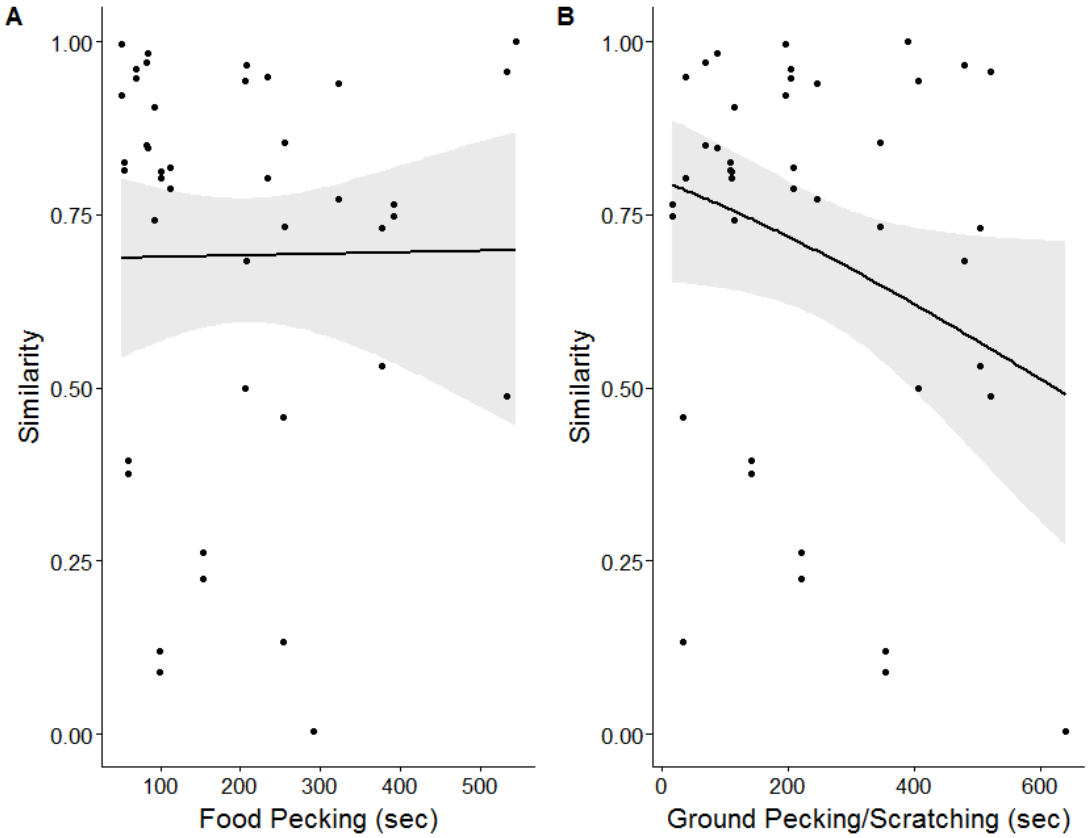



Figure 7.A.1: *Similarity* between the chicks' and hens' foraging decisions given the *amount of food pecking* (A), and *ground pecking and scratching* (B) by the hen. The line is a fitted glm model with the quasi-binomial family. The shaded band is the 95% C.I. on the fitted values

**Appendix 7.B:** Analysis of the chicks' pecking behaviour during the colour preference tests based solely on the hens' pecking behaviour during conditioning

When fitting the model only with the *proportion of time spent pecking by hens at the coloured food consistent with the chicks'*, there was no evidence that the *proportion of time spent pecking by chicks at the coloured food consistent with their training* was affected by the *proportion of time spent pecking by hens at the coloured food consistent with the chicks' training* ($F = 2.59$, d.f. = 42, $p = 0.115$; see Table 7.B.1 and 7.B.2).

Table 7.B.1: Summary of the linear mixed model fitting the *proportion of food eaten by the chicks that is consistent with their training during the test period* given the *proportion of food eaten by the hens that is consistent with the chicks' training during conditioning*

| Variable | Estimate | Std Error | 95% C.I. | DF | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | -2.14 | 0.93 | -3.96, -0.32 | 132 | -2.30 | 0.022 |
| Hen Prop Consistent Chick Training During Conditioning | 2.30 | 1.43 | -0.50, 5.10 | 42 | 1.61 | 0.115 |

Table 7.B.2: Anova of the linear mixed model fitting the *proportion of food eaten by the chicks that is consistent with their training during the test period* given the *proportion of food eaten by the hens that is consistent with the chicks' training during conditioning*

| Variable | Num DF | Den DF | F-value | p-value |
|---|---|---|---|---|
| (Intercept) | 1 | 132 | 3.26 | 0.073 |
| Hen Prop Consistent Chick Training During Conditioning | 1 | 42 | 2.59 | 0.115 |

Similar effects were found for the number of pecks (*proportion of pecks by hens on coloured food consistent with the chicks' training* ($F = 1.88$; $p = 0.178$)) and for pecking rate (*proportion of pecks by hens on coloured food consistent with the chicks' training* ($F = 3.00$; $p = 0.090$)).

**Appendix Chapter 8:**

**Appendix 8.A:** Summary of the results of the randomisation tests for the insertion, eating, and interaction behaviour of the food-offering call experiment (Chapter 6) for all individuals (Table 8.A.1) and non-juveniles only (Table 8.A.2) (as opposed to the results of just the juveniles reported in Chapter 6)

Table 8.A.1: p-values of randomisation tests (and effect sizes) for all individuals

| Behaviour /Part | Phase 1 (Training) | Phase 2 (Testing) |
|---|---|---|
| Insertion | 0.427 (r=0.144) | 0.320 (r=0.184) |
| Eating | 0.797 (r=0.046) | 0.305 (r=0.196) |
| Interaction | **0.033 (r=0.386)** | 0.847 (r=0.037) |

Table 8.A.2: p-values of randomisation tests (and effect sizes) for non-juveniles only

| Behaviour /Part | Phase 1 (Training) | Phase 2 (Testing) |
|---|---|---|
| Insertion | 0.990 (r=0.004) | 0.616 (r=0.124) |
| Eating | 0.384 (r=0.176) | 0.678 (r=0.106) |
| Interaction | 0.187 (r=0.279) | 0.366 (r=0.213) |